TROPHIC PATHWAYS SUPPORTING JUVENILE CHINOOK AND COHO SALMON IN THE GLACIAL SUSITNA RIVER, ALASKA: PATTERNS OF FRESHWATER, TERRESTRIAL, AND MARINE RESOURCE USE ACROSS A SEASONALLY DYNAMIC HABITAT MOSAIC

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A

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Abstract

In large, seasonally dynamic and spatially complex watersheds, the availability and relative importance of various food resources for stream fishes can be expected to vary substantially. While numerous studies have attempted to uncover the trophic linkages that support stream salmonids, much of these efforts have occurred at small scales that disregard variability of food resources inherent in lotic systems. This study aimed to determine large-scale patterns in the contributions of freshwater, terrestrial, and marine-derived food resources to juvenile Chinook and Coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*) in the large, glacially influenced Susitna River, Alaska. I quantified diet patterns both spatially, across different macrohabitat types positioned along a 169-km segment of the river corridor, and temporally, from June to October, using stable isotope and stomach content analyses. To further resolve energy pathways from basal carbon sources to juvenile salmon, I determined the relative roles of terrestrial organic matter and freshwater periphyton food sources to aquatic benthic invertebrate diets. The latter analysis showed that invertebrate consumers were more reliant on freshwater periphyton than on terrestrial organic matter. Bayesian stable isotope mixing models indicated that juvenile salmon in the middle Susitna River were, in turn, largely supported by freshwater invertebrate prey regardless of spatial and temporal context. The relative contribution of marine-derived prey (salmon eggs) to juvenile salmon diets was greatest in the fall within tributary mouth and off-channel macrohabitats during both years of the study. Terrestrial invertebrate prey contributions were generally greatest during mid-summer within all macrohabitat types sampled, however this pattern varied across years. No upstream to downstream diet pattern was apparent from the data. These results underscore the importance of freshwater energy pathways for sustaining juvenile Chinook and Coho salmon in the Susitna

River and provide further spatial and temporal context for the importance of pulsed marine and terrestrial prey subsidies. As Pacific salmon stocks continue to decline, management and mitigation efforts should operate on knowledge gained from studies that encompass the large-scale spatial and temporal variability inherent in riverine landscapes.

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Chapter 1. General Introduction

Studying the diet patterns of organisms provides insight into the ecological processes affecting their growth and survival. Investigating juvenile Pacific salmon (*Oncorhynchus* spp.) diet patterns in riverine habitats, however, is an arguably complex endeavor given the heterogeneous and dynamic nature of lotic systems and the propensity of these fish to utilize multiple habitats to maintain an overall positive energetic balance (Armstrong et al. 2010). Studies that have focused on juvenile salmonid feeding patterns in river systems have largely focused on the composition of prey in stomach contents and mechanism of feeding at relatively small spatial and temporal scales, not accounting for the potential variability in consumer diets across the seasonally dynamic riverine habitat mosaic (but see Doucett et al. 1996; Bellmore et al. 2013). This gap in knowledge is concerning, as salmon-bearing river systems continue to be altered by riparian land use, hydrological modifications, and climate change. Without addressing salmon trophic ecology at larger spatial and temporal scales, a broader understanding of the importance of their various food resources is incomplete and may not be relevant to management and conservation problems that typically operate at larger spatial and temporal scales (Fausch et al. 2002).

Numerous studies investigating the diets of stream fishes on single-habitat or reach scales have uncovered the importance of multiple energetic pathways for sustaining stream fishes. Freshwater benthic invertebrates, such as aquatic flies (Diptera), mayflies (Ephemeroptera), and stoneflies (Plecoptera) have long been recognized as a staple food source for juvenile salmonids (Allen 1951; Hynes 1970). Several studies in Alaska have demonstrated that larval and emerging benthic invertebrates, especially Dipteran chironomids of all life stages, were the primary food source for juvenile salmon (Loftus and Lenon 1977; Hansen and Richards 1985; Sagar and

Glova 1987; Gutierrez 2011), and when production and availability of benthic invertebrates increased via experimental nutrient fertilization, fish growth and production also increased (Johnston et al. 1990; Harvey et al. 1998). Production and availability of freshwater invertebrates can vary widely, from 10^0 to 10^3 g dry mass m^{-2}, with the lowest production across river systems occurring in cool-temperate and arctic streams due to low temperature and food limitation (Huryn and Wallace 2000).

Riparian zones play a major role in regulating energy flow in river systems by transporting nutrients, plants, and animals that are utilized by organisms at many trophic levels in freshwater food webs (Vannote et al. 1980; Naiman and Décamps 1997). For stream fishes in particular, terrestrial invertebrates can be a major food resource (Nielsen 1992; Wipfli 1997; Kawaguchi and Nakano 2001; Allan et al. 2003) when they fall into riverine habitats from overhanging vegetation in surrounding riparian areas or are imported via bank erosion and overland flow (Edwards and Huryn 1995). Terrestrial insect inputs into fish foraging areas are highly variable across seasons, with the highest rates often occurring during mid-summer when insects are most active and abundant (Wipfli 1997; Nakano and Murakami 2001). Inputs of terrestrial insects are also dependent on factors such as forest and plant cover types, temperature, and weather (Price 1997). Streamside vegetation type is speculated to play a major role in the amount, timing, and type of terrestrial insects that fall into streams; specifically, the presence of broad-leafed deciduous species can increase the input of terrestrial insects into streams because they provide more surface area for insects than the small needles of conifers (Wipfli 1997; Allan et al. 2003).

Upon returning from marine environments, spawning Pacific salmon can deliver large pulses of marine-derived nutrients and energy to many organisms in riverine food webs (Wipfli

et al. 1998; Cederholm et al. 1999; Chaloner and Wipfli 2002). Their carcasses, eggs, and emergent fry can serve as a significant food resource for stream fishes in particular (Bilby et al. 1998; Moore et al. 2008; Armstrong et al. 2010; Rinella et al. 2013). Salmon eggs become available as prey items for stream fishes when spawning occurs at a sufficiently high density so that females compete for nest space by digging out another female's nest and dislodging buried eggs (Moore et al. 2008).

Stream salmonids are known to be opportunistic predators, readily capitalizing on energetically favorable prey. Selective foraging by stream salmonids on terrestrial prey has been documented in several studies, presumably because terrestrial insects generally have larger body sizes and higher energy contents relative to freshwater invertebrates (Cummins and Wuycheck 1971), conferring a greater energetic benefit upon consumption (Nielsen 1992; Nakano et al. 1999; Rosenfeld and Raeburn 2009). In experimental stream reaches, for example, juvenile Coho Salmon diets were found to contain terrestrial invertebrates at elevated proportions compared to the food types available in the environment (Nielsen 1992; Rosenfeld and Raeburn 2009). Juvenile salmon with sufficiently large gape sizes have also been observed preferentially consuming salmon eggs (Bilby et al. 1998; Armstrong et al. 2010) when they become present, again presumably because they are extremely energy rich (~ 18,000 J/g^{-1} per salmon egg vs. ~2,000 J/g^{-1} per invertebrate, Quinn et al. 2012), easily handled and digestible, and highly visible with their bright orange color (Armstrong et al. 2010). This combination of attributes makes salmon eggs an energetically more profitable prey source than invertebrate prey, and preferentially consuming this resource when available likely maximizes energy intake.

In large, seasonally dynamic river networks, the availability and relative importance of freshwater, marine, and terrestrial food resources for stream fishes can be expected to vary

substantially across the diverse landscape (Stanford et al. 2005). The magnitude and quality of prey pulses from these ecosystems is influenced by many interrelated biological and physical factors, many of which are strikingly seasonal. In temperate stream reaches, benthic invertebrate production and emergence is often highest in late winter and early spring (Nakano and Murakami 2001). Fluxes of terrestrial invertebrate prey to stream habitats often peak during mid-summer when terrestrial productivity is at its highest (Wipfli 1997; Nakano and Murakami 2001; Baxter et al. 2005), and marine-derived resource pulses are likewise markedly seasonal and typically peak in late-summer and fall as freshwater and terrestrial invertebrate production is declining (Wipfli and Baxter 2010). These general seasonal patterns may also be modified by spatial relationships to the source of prey; for example, the position of fish habitat relative to the mouth of the river network during spawning salmon migration may strongly influence the magnitude and duration of marine-derived prey that is ultimately available for fish consumption (Wipfli and Baxter 2010). Additionally, the availability of pulsed prey subsidies may be modified further by the physical conditions of a given habitat (e.g. water velocity, turbidity) and the rate at which subsidies flow across its boundaries (Wiens 2002). Taking these drivers of food resource availability into account, it becomes clear that understanding the diet patterns of juvenile salmonids in their freshwater stage must encompass the variability that is inherent in complex, dynamic river systems.

The work conducted in my research project examined large-scale spatial and temporal diet patterns of juvenile Chinook and Coho salmon within the glacial Susitna River in Southcentral Alaska, U.S.A. Using stable isotope and stomach content analyses, I quantified the relative contributions of freshwater, marine, and terrestrial food resources both spatially, across different macrohabitat types positioned along a 169-km segment of the river corridor, and seasonally,

from June to October. Additionally, I examined the relative contributions of the two potential energy sources, terrestrial organic matter and freshwater periphyton, to freshwater invertebrates to more fully resolve energy pathways from basal carbon sources to juvenile salmon.

This study was conducted for the Susitna-Watana Hydroelectric Project, and was intended to provide baseline stable isotope data against which post-dam construction and operation conditions can be evaluated. Regulated flows and other impacts from dam operations may have implications for the suitability of the physical habitats and the availability of food resources that ultimately contribute to salmon productivity while they rear in riverine habitats. Understanding the present state of seasonally dynamic riverine habitats and trophic relationships that support salmon may help resource managers and dam operators on the Susitna to identify habitat types that support the most productive aquatic communities and how they may be affected by altered flows and temperature regimes.

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Chapter 2. Trophic pathways supporting juvenile Chinook and Coho salmon in the glacial Susitna River, Alaska: patterns of freshwater, terrestrial, and marine resource use across a seasonally dynamic habitat mosaic[1]

2.1 Abstract

Riverine landscapes consist of a mosaic of habitats that receive food subsidies from terrestrial, freshwater, and marine environments. The contributions of these resources to rearing Chinook and Coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*) can shift over time and space, altering the energy pathways that limit fish production. Despite the need for understanding drivers of salmonid production, most riverine food web research has operated on small spatial scales and does not account for the broader heterogeneous nature of the entire river network. This study aimed to determine large-scale patterns in contributions of terrestrial, freshwater, and marine food sources to juvenile salmonids in the glacially influenced Susitna River, Alaska. We quantified trophic patterns spatially, across different macrohabitat types positioned along a 169-km segment of the river corridor, and temporally from June to October, using Bayesian stable isotope mixing model and stomach content analyses. To further resolve energy pathways from basal carbon sources to juvenile salmon, we determined contributions of terrestrial organic matter and aquatic periphyton to freshwater invertebrate primary consumer feeding groups. The latter analysis showed that all invertebrate feeding groups were more reliant on freshwater periphyton than on terrestrial organic matter. Mixing models indicated that juvenile salmon in the middle Susitna River were, in turn, largely supported by freshwater invertebrate prey regardless of spatial and temporal context. The relative contribution of marine-derived prey (salmon eggs) was greatest in the fall within tributary mouth and off-channel habitats, whereas the contributions of terrestrial invertebrate prey were generally greatest during mid-summer

within all macrohabitat types sampled. No upstream to downstream diet pattern was apparent from the data. These results highlight the overall significance of the freshwater energy pathway to consumers and provide large-scale spatial and seasonal context for the importance of pulsed marine and terrestrial prey subsidies to juvenile Chinook and Coho salmon throughout the middle Susitna River. Understanding broad patterns and dynamics of food resource contributions to rearing juvenile salmonids can assist in improved management decisions of stream salmonid populations, their habitats, and the ecosystems from which their food subsidies originate.

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2.2 Introduction

Riverine landscapes consist of a mosaic of dynamic habitats, wherein aquatic consumers receive energy and nutrients from a number of ecologically distinct sources. Consumers within salmon-bearing streams and rivers in particular can assimilate energy and nutrients that originate from freshwater, terrestrial, and marine ecosystems, however the relative importance of these resources to consumers may vary drastically over time and space (Wipfli and Baxter 2010). As generalist predators, juvenile Pacific salmon (*Oncorhynchus* spp.) are known to capitalize on ephemeral pulses of prey from these different ecosystems (Wipfli 1997; Bilby et al. 1998; Reichert et al. 2008; Armstrong et al. 2010) in order to maximize energy intake and growth, thus conferring a much-needed advantage before entering into the marine environment (Bilton et al. 1982; Henderson and Cass 1991). While many studies have quantified the diet composition and foraging behavior of juvenile salmon in streams (Nielsen 1992; Harvey and Railsback 2013; Piccolo et al. 2014), less is understood about the variability of food resource use over larger temporal scales and across the diverse riverine landscape (Fausch et al. 2002; Wipfli and Baxter 2010). Given the continuing declines of many high-latitude Pacific salmon populations (NRC 2004; Alaska Department of Fish and Game 2013), there is a need to more thoroughly understand the trophic relationships that support their production during freshwater rearing.

On a broad landscape level, the availability of prey resources and their contributions to juvenile salmonid production may be governed by seasonal changes in abundance (e.g. Wipfli 1997; Nakano and Murakami 2001), physical and biological conditions within distinct habitats (Armstrong et al. 2010; Bellmore et al. 2013), and distance from the mouth of the river (Vannote et al. 1980; Doucett et al. 1996; Wipfli and Baxter 2010). At higher latitudes, relatively extreme seasonal fluctuations produce markedly pulsed life history patterns that can translate to episodes

of increased food availability (Yang et al. 2008) to stream fishes. Both freshwater and terrestrial invertebrate abundance in streams can be highly variable across seasons. In temperate streams along the Pacific Rim, these prey resources have exhibited temporally-offset peaks in availability and use by salmonids, with the greatest influence of freshwater invertebrates in late winter through early summer, followed by terrestrial invertebrates during mid- to late-summer (Wipfli 1997; Nakano and Murakami 2001). Seasonal pulses in food resources are also manifested through the upstream migration of anadromous salmon during early summer through autumn, producing a pulse of nutrients and energy to stream food webs that can increase productivity beyond in-situ background levels (Kline et al. 1990; Wipfli et al. 1998, 1999; Chaloner and Wipfli 2002). While subsidies from spawning salmon are usually short-lived within a reach, consumption of the energy-rich eggs and carcass tissue by fish can supplement growth later in the season while other food sources are low in abundance (Bilby et al 1998; Wipfli et al. 2003; Wipfli and Baxter 2010).

Marked variations in energy flow to fish populations can occur broadly, along an upstream to downstream continuum within a river network (Vannote et al. 1980). For example, stable isotope analysis was used to determine the percent terrestrial carbon that contributes to juvenile Atlantic Salmon (*Salmo salar*) along a river gradient in New Brunswick. Their results showed that downstream fish populations derived less of their dietary carbon from terrestrial sources than fish in headwaters (Doucett et al.1996), consistent with the River Continuum Concept (Vannote et al. 1980). Several authors (Polis et al. 1997; Baxter et al. 2005; Wipfli and Baxter 2010) have hypothesized an exception to a longitudinal gradient in food resources, such that highly braided floodplains lower down in the watershed with relatively large perimeter to area ratios may be exposed to an increase in terrestrial subsidies, especially during high flows.

The overall effect could therefore confound obvious longitudinal trends in the contribution of terrestrial carbon to stream food webs. Anadromous fish runs could also affect juvenile salmon populations differentially along the river corridor if, for example, habitats closer to the river mouth have greater densities of spawning salmon, and therefore a greater subsidy of eggs and carcass tissue available for consumption (Wipfli and Baxter 2010). A longitudinal effect would therefore be expected to be highly variable across ecosystems, depending on the species of salmon present, the relative strength of their runs, and the spatial relationship between suitable spawning and rearing habitat (Wipfli and Baxter 2010). The trophic ecology of fish as it relates to longitudinal variation in river networks has gained some attention, but empirical studies at large spatial scales are rare.

The diverse nature of habitats within riverine landscapes can also produce fine-scale spatial variability in food resource contributions to consumers. In contrast to the longitudinal predictability posited in the River Continuum Concept, Poole (2002) proposed that food webs within any particular habitat are not necessarily more similar to those in adjacent habitats than they are to those located in distant upstream or downstream reaches. Because riverine habitats differ in the biotic and abiotic features and processes that control instream primary production as well as the influx of organic matter and prey subsidies, they are likely to contain food webs that are distinct from others in close proximity (Wiens 2002; Winemiller 2005). In the Methow River, U.S.A., the connectivity of different floodplain habitats influenced variability in the production and flux of freshwater and terrestrial invertebrate prey, ultimately leading to variability in the diet compositions of juvenile Chinook Salmon and other fish species across habitats (Bellmore et al. 2013). Additionally, when spawning habitat is limited, females are driven to superimpose their nests on preexisting ones and release previously buried eggs in the process (Briggs 1953;

Fukushima et al. 1998; Essington et al. 2000). Thus, even small increases in adult salmon density beyond a certain threshold can drive disproportionately large increases in egg availability and consumption by stream fishes (Moore et al. 2008). In habitats where suitable spawning area is limited relative to the number of spawners, there would likely be a greater magnitude of marine subsidies available for rearing salmon compared to other habitats in the riverine landscape where densities of spawning salmon are lower.

The hydroecological dynamics of glacial-fed river systems introduce additional complexity in understanding salmonid trophic patterns relative to the temperate snowmelt- and precipitation-dominated systems where the majority of juvenile salmon feeding ecology studies have been conducted. In contrast to these snowmelt/precipitation-dominated regimes where discharge generally peaks in both spring and late fall, peak glacial melt typically occurs during mid-summer with higher air temperatures (Milner and Petts 1994). During this time, increased suspended loads of fine sediment and glacial flour scours wetted substrates and limits light penetration to benthic algae (Lloyd 1987). Studies in glacial rivers have shown that benthic algal and macroinvertebrate productivity was greater during spring and autumn, before and after the peak glacial melting period when environmental conditions were relatively benign (Burgherr and Ward 2001; Fureder et al. 2001; Uehlinger et al. 1998; Milner et al. 2009). The effect of sediment on benthic communities would then likely control the contribution of freshwater-derived carbon to juvenile salmon rearing in glacial habitats (Perry et al. 2003), but this pattern across multiple glacial and non-glacial habitats has not been investigated to date. An improved understanding of the variability in juvenile salmon trophic relationships across diverse, glacially influenced river systems is needed to predict how riparian land use, migration barriers, and flow

alterations due to climate change and human activities in such systems might influence their productivity.

In this study, we address how the relative contributions of freshwater, terrestrial, and marine-derived dietary resources to juvenile Coho and Chinook (*O. kisutch* and *O. tshawytscha*) salmon vary within a 169-km section of the large, glacial Susitna River in Southcentral Alaska, U.S.A. Specifically, we address variability of these resource contributions both spatially, across different macrohabitat types positioned along a 169-km segment of the river corridor, as well as temporally, from June to October. In addition, we apply a broad-scale $\delta^{13}C$ stable isotope analysis to characterize the relative contributions of instream and terrestrial carbon sources to freshwater invertebrate primary consumers. This supplementary analysis will provide further understanding of energy flow at the base of food webs in the Susitna River and therefore a greater understanding of energy sources contributing to fish. By quantifying current patterns of energy flow in a large, glacial river, this study represents an important step towards predicting how future landscape or climatic changes may affect the trophic processes supporting juvenile salmonids in such systems.

2.3 Methods

2.3.1 Study area

Field sampling took place in 2013 and 2014 on the Susitna River in Southcentral Alaska. This 504-km river drains a 52,000-km^2 catchment headed by several glaciers in the eastern Alaska Range and flows southwest into the Cook Inlet west of Anchorage (Fig. 2.1). The river had a characteristic glacial melt and snowmelt hydrological regime with low flows and ice cover in winter, peak flow during snowmelt in late May and June, and sustained flows from glacial

runoff throughout summer. Main channel discharge at river kilometer 225 peaked on June 2nd (2,568 m^3 s^{-1}) in 2013 and on June 27th (1,206 m^3 s^{-1}) in 2014.

A total of 16 sampling sites were located within four reaches between 129 and 298 river kilometers from the mouth of the Susitna River (Fig. 2.1). Within each reach we selected sites within glacial-fed main channel and side channel macrohabitats as well as available off-channel macrohabitats that may have included a tributary mouth, side slough, or upland slough (Table 2.1). The uppermost reach (Reach 4) at river kilometer 296 was located within an approximately 238-m wide bedrock-bounded canyon and contains a main channel, side channel, and tributary mouth sampling site. A set of Class VI rapids, known as "Devils Canyon", between river kilometer 241 and 259 differentiated this upstream reach from those below it by acting as a migration barrier for the majority of anadromous salmon (LGL Alaska Research Associates and ADF&G, 2014). The next reach downstream (Reach 3) at river kilometer 227 was located in a wider canyon segment that averages 716 m in width and contained a main channel, side channel, tributary mouth, and upland slough sampling site. At river kilometer 167, Reach 2 was located within a primarily single-channel floodplain with numerous interconnected off-channel habitats, and had an average active channel width of 344 m. Here, we sampled within a main channel, side channel, tributary mouth, side slough, and upland slough site. At river kilometer 130, Reach 1 was the study section closest to the river mouth and was located in the highly braided floodplain below the confluence of the Susitna, Chulitna, and Talkeetna Rivers, where the average active width was 951 m. This reach contains a main channel, side channel, tributary mouth, and upland slough site. To characterize seasonal variation in juvenile salmon diets, we visited the aforementioned macrohabitats located within each study reach three times during the open-water period, and designated these periods as spring, summer, and fall (Table 2.2). Logistical

difficulties in 2013 precluded sampling at all study sites during all seasons, however all study sites were sampled in 2014.

2.3.2 Sample collection and preparation

To elucidate large-scale patterns in the diet sources of juvenile salmon and primary consumer invertebrates, we collected samples from juvenile Chinook and Coho salmon, their potential diet items, and basal carbon sources for stable isotope analysis. Freshwater periphyton and terrestrial organic matter are considered basal resources for aquatic invertebrates (Finlay 2001). We collected three periphyton samples per site by selecting five non-embedded rocks from three representative areas of the site and scrubbing the entire surface with a brush. We then rinsed samples into a container using distilled water and stored them in a cooler until they could be frozen (typically within six hours). Conditioned terrestrial organic matter (OM) is a potentially major food source to some aquatic invertebrates and has been shown to be an adequate isotopic representation of terrestrial carbon (Finlay 2001). At sites with sufficient flow, we collected two OM seston samples by setting two drift nets with 250-µm mesh at the upstream end of each site, positioning the tops of the nets above the surface of the water and the bottom of the nets off the substrate, for a period of 45 min to 3 hr depending on how quickly the nets became full with material. At sites with little or no flow, we collected the two seston samples by actively moving a 250-µm D-frame kick net across the surface of the water in two representative areas until enough mass was obtained for stable isotope analysis. We also collected three samples of OM embedded in the substrate with a Hess sampler (250-µm mesh) when there was sufficient flow by embedding the sampler deep enough in the substrate in order to create a seal and then disrupting the substrate by hand. When flows were not sufficient we used a 250-µm

mesh kick net, again disrupting the substrate. We targeted terrestrial and aquatic invertebrates at each site as representative food items for juvenile salmon that were caught in the same location by collecting and packaging with OM samples, to be sorted later in the laboratory. We opportunistically collected spawning salmon carcasses and eggs when they were present to represent marine-derived food sources for juvenile salmon. If a salmon carcass was reasonably fresh, we excised 2 - 5 g of white muscle tissue, and salmon eggs were stored whole. Because freezing stable isotope samples was logistically infeasible, we preserved all OM, invertebrate, and marine-derived samples on site with 70% ethanol. The tested effects of ethanol preservation on stable isotope values have shown mixed results across recent studies, however most of these studies reported insignificant shifts in $\delta^{13}C$ and $\delta^{15}N$ values relative to samples that were immediately dried or frozen (Feuchtmayer and Grey 2003; Syväranta et al. 2008), especially if the solution did not exceed 70% ethanol (Hobson et al. 1997; Barrow et al. 2008; Gloutney and Hobson 1998).

To determine juvenile Chinook and Coho salmon diet, we collected both their stomach content samples and caudal fin tissues for stable isotope analysis. Stomach content analysis and stable isotope analysis are complementary techniques that have been used to quantify food resource contributions in lotic systems (Doucett et al. 1996; Wipfli 1997; Bellmore et al. 2013). Stomach content analysis allows fine-scale identification of undigested prey items and a snapshot of a consumer's recent diet; however, this method has some important limitations, especially for studies focused on broad-scale trophic relationships. Prey may digest and assimilate into consumer tissue at variable rates (e.g. highly scleritized vs. fleshy invertebrates) and in general may be unrecognizable, therefore skewing results and interpretations (Baker et al. 2014). Because this method only provides a recent picture of feeding patterns, researchers cannot

extrapolate findings beyond a few days, especially when food resources are temporally variable (Woodward and Hildrew 2002). $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis overcomes some of these problems because it provides a time-integrated measurement of assimilated prey sources present in consumer tissue (Peterson and Fry 1987). When food sources have distinct isotopic signatures, ecologists can assess the relative contributions of each potential food resource to a consumer. Even though stable isotope analysis has expanded the abilities of stream ecologists to track energy and nutrients through food webs, $\delta^{13}C$ signatures of freshwater carbon sources can be highly variable (Finlay 2001) and oftentimes difficult to distinguish from terrestrial energy sources (Rounick and Winterbourn 1986). In addition, the accuracy of this technique has been questioned due to variable diet-tissue fractionation among ecosystems and species (Wolf et al. 2009). Recent advances in Bayesian stable isotope mixing models address these shortcomings by allowing the combination of stable isotope and stomach content data, as well as by incorporating variable nutrient concentrations and error in fractionation values (Moore and Semmens 2008; Parnell et al. 2010). The most advanced Bayesian mixing model to date, MixSIAR (Stock and Semmens 2013), includes these features and should therefore be able to characterize relative food source contributions with greater accuracy than has been attained before.

At each site, we sampled up to eight juvenile Chinook and eight juvenile Coho salmon that measured at or above 50 mm fork length. We deemed sampling procedures too harmful for smaller individuals (Sanderson et al. 2009). We used a variety of active and passive fish capture methods across macrohabitat types, which included beach seining, backpack electrofishing, and deploying fyke nets and minnow traps. Before sampling, we anesthetized fish using a clove oil-ethanol solution or Aqui-S 20E (AquaTactics Fish Health). Once individuals exhibited a loss of equilibrium we measured mass and fork length and obtained stable isotope samples from fish by

excising a 1-3 cm^2 portion of the lower caudal fin lobe (Hanisch et al. 2010) and subsequently placed samples in Eppendorf tubes with 70% ethanol solution. We chose to target caudal fin tissue for stable isotope analysis because it is a rapidly regenerating tissue (Hanisch et al. 2010) with a relatively fast turnover time of approximately 13 days for small salmonid fry (Heady and Moore 2013). We sampled stomach contents by non-lethal gastric lavage (stomach flushing) through a modified syringe (Culp et al. 1988). We stored stomach content samples in 70% ethanol to be later enumerated in the laboratory. Once sampling was complete we held fish in a recovery container until equilibrium and responsiveness was regained.

2.3.3 Laboratory methodology and sample preparation

2.3.3.1 Stable isotope samples

We rinsed, dried (at least 72 hrs at 60° C), and ground all stable isotope samples into a homogenous powder. In preparation for stable isotope analysis, we thawed and filtered periphyton samples and removed any invertebrates and other visible contaminants, then fumed periphyton samples in HCl for 4 hrs to remove any carbonates originating from rock substrates (Harris et al. 2001). We examined benthic and seston samples under a dissecting microscope and removed any invertebrates found, and identified them to a taxonomic level necessary to distinguish between freshwater and terrestrial origin following Merritt and Cummins (2008). We further identified and separated aquatic invertebrates into functional feeding groups (collectors, grazers, predators, and shredders) in order to resolve energy flow pathways from basal food web carbon sources (Merritt and Cummins 2008). Most functional feeding group samples contained 2 to > 50 individuals, however we occasionally used a single individual if no other individuals were found and if the individual exceeded 0.2 mg required for analysis. After drying and

grinding but before analysis, we treated invertebrate, salmon carcass, and egg samples with a 2:1 chloroform-methanol solution to remove lipids, which typically have more variable and depleted $\delta^{13}C$ signatures relative to other tissue types (Sotiropoulos et al. 2004). We expected that lipids in invertebrate sample tissues would hydrolyze in the ethanol preservative at varying rates depending on body size, therefore we deemed lipid-extraction necessary in order to standardize lipid content.

We subsampled and weighed all samples on a micro-analytical balance (readability = 0.001 mg) and placed them into tin capsules at the Alaska Stable Isotope Facility (University of Alaska Fairbanks). We analyzed all samples via combustion using an elemental analyzer (Costech Analytical) interfaced to an isotope ratio mass spectrometer (DeltaV^{plus}XP CF-IRMS, Thermo Fischer LLC) in continuous flow mode, and determined mean analytical precision using laboratory standards (Sigma Chemical; mean $\delta^{15}N$ = 6.95‰ and mean $\delta^{13}C$ = -15.82‰). Instrument precision was 0.11‰ for $\delta^{15}N$ and 0.05‰ for $\delta^{13}C$.

2.3.3.2. Juvenile salmon stomach content samples

We identified invertebrate prey items encountered in fish stomach content samples to family and life stage (larva, pupa, adult) if possible following Merritt and Cummins (2008), and by their environment of origin (freshwater or terrestrial). We identified prey fish to the lowest possible taxonomic level, and measured the total lengths (mm) of intact prey items directly. We estimated total lengths for partially digested prey based on intact items of the same taxon that appeared similar in size, or by using the weighted average of lengths of that taxon in the same sample, site, macrohabitat, reach, or season.

2.3.4 Statistical analysis

2.3.4.1 Freshwater invertebrate energy source contributions

We used multiple linear regressions to determine the role of terrestrial OM and periphyton in the diets of the invertebrate collector, grazer, and shredder primary consumer groups. Periphyton $\delta^{13}C$ can be highly variable within reaches and can often overlap with that of terrestrial OM within a given site, however stable isotope mixing models require distinct endmembers to determine precise dietary contribution estimates. Therefore, using site-specific mixing models to estimate resource contributions of periphyton and terrestrial OM to invertebrate consumers would likely produce unacceptable error in some cases. Previous studies (Finlay 2001, Bunn et al. 2003, Rasmussen 2010, Jardine et al. 2014) have used a gradient method wherein spatial variation of source and consumer $\delta^{13}C$ is used to determine overall, large-scale contributions of freshwater algae (or periphyton) and terrestrial OM to invertebrate primary consumers. To understand large-scale energy flow to aquatic invertebrates, we performed multiple linear regressions between site-specific mean $\delta^{13}C$ values of primary consumer feeding groups (collectors, grazers, and shredders) and site-specific mean $\delta^{13}C$ values of their potential food sources (periphyton and terrestrial OM) collected from all locations. Mean $\delta^{13}C$ values of terrestrial OM collected in the stream benthos (-28.0 ± 1.4‰) and in seston samples (-27.8 ± 1.2‰) did not differ significantly (Kruskal-Wallis H Test: $H = 11.98$, $p = 0.46$), so these sample types were pooled as a single terrestrial OM food source. Sample material from some consumer feeding groups was limited or not available at certain sampling events, so we pooled all consumer $\delta^{13}C$ values across seasons. Each data point in the regressions therefore represents the mean $\delta^{13}C$ value of a consumer group and source (either periphyton or terrestrial OM) collected from a particular site across all seasons in which sample material was available.

We analyzed data from each year separately in order to detect differences in the contributions of periphyton and terrestrial OM on primary consumer groups between years with dissimilar flows. Because there is little isotopic fractionation of organic carbon from prey to consumer (DeNiro and Epstein 1978), a slope coefficient close to 1 and a high r^2 value indicates a strong reliance on a particular food source (Finlay 2001; Jardine et al. 2014). Prior to conducting analysis on basal carbon sources, we evaluated possible cross-contamination between the two food source sample types by comparing C:N concentration ratios with those reported in literature sources. Periphyton C:N typically ranges from 8:1 (Thorp et al. 1998) to 12:1 (Wetzel 1983) and terrestrial OM (soil organic matter and terrestrial plants) C:N ranges from 8:1 to > 50:1 (Finlay and Kendall 2007). Both the mean periphyton and mean terrestrial OM C:N values approximated the known values (mean $C:N_{periphyton}$ = 8.7 ± 2.8 SD; mean $C:N_{OM}$ = 29.8 ± 9.4 SD), suggesting that these samples sufficiently represented their designated sources; however, it is still possible that some cross-contamination occurred. Regressions were conducted using R.3.1.1 (R Development Core Team, 2014). For all tests, $\alpha = 0.05$.

2.3.4.2 Juvenile salmon stomach content analysis

We calculated the composition of freshwater, marine, and terrestrial diet items as well as the most common invertebrate taxa in stomach samples as diet proportions by dry mass (% mean mass), the most applicable metric for energy flow and food web studies (Chipps and Garvey 2007). We determined terrestrial and freshwater invertebrate dry mass using the allometric formula:

$$W = aL^b,$$

where W is the total dry body mass, L is the total body length, and a and b are the constants of the regression between W and L (Ricker 1973). We derived length-mass regression constants a and b from the literature (Rogers et al. 1976, 1977; Smock 1980; Benke et al. 1999; Johnston and Cunjak 1999; Sabo et al. 2002) and from recent unpublished data from Alaskan stream invertebrates (M. Wipfli, UAF). We also used length-mass relationships to estimate the wet mass for prey fish using taxon-specific length and mass measurements (2013 field data from Middle and Lower Susitna River Fish Distribution and Abundance Study, Alaska Energy Authority, AEA) as well as for salmon eggs using published values (Fleming and Ng 1987). We then used the resulting wet mass of prey fish and salmon eggs to estimate dry mass using percent dry mass values of 24.9% for *Oncorhynchus* spp., 22.5% for sculpins, and 40% for fresh salmon eggs (Brey et al. 2010; Ashton et al. 1993).

2.3.4.3 Juvenile salmon diet modeling

We estimated the relative contributions of freshwater, marine, and terrestrial prey to salmon diets from stable isotope and stomach content data using the Bayesian stable isotope mixing model, MixSIAR (Stock and Semmens 2013). This model uses isotopic values of consumers, prey, and trophic enrichment factors as model inputs. MixSIAR estimates the probability distributions of multiple prey contributions to consumers while accounting for the observed variability in consumer, prey, and trophic enrichment isotopic values (Stock and Semmens 2013). The model also allows the incorporation of prior information from another dietary dataset, such as stomach content data, to further refine estimates of prey contributions to a consumer (Moore and Semmens 2008; Parnell et al. 2010). We chose to incorporate informative priors from stomach content data to mitigate potential temporal biases of these two

methods and to obtain more precise estimates when prey sources are isotopically similar or sample sizes were low. The posterior model outputs presented in this study are therefore a combination of the priors and the maximum likelihood influence of the isotopic data, where prey sources that are well-separated (less correlated) in isotopic space ($\delta^{15}N$ vs. $\delta^{13}C$) provide more useful information for the isotopic data to override influence from priors (Moore and Semmens 2008). Conversely, when the prey sources are isotopically more similar (highly correlated), priors may have more influence in the posterior output (Moore and Semmens 2008). We calculated prior values separately for each sampling event by multiplying the diet proportion of each prey type (freshwater, terrestrial, or marine) by the sample size of non-empty stomachs. Correlations between posterior estimates of diet proportions are reported for diagnostic purposes in the discussion as Pearson's product-moment correlation coefficients (r).

To select appropriate trophic enrichment factors (TEF; Δ) for diet modeling, we qualitatively evaluated consumer isotopic signatures relative to those of the potential prey after adjusting for TEF values from four different literature sources (VanderZanden and Rasmussen 2001; Post 2002; McCutchan et al. 2003; and Trueman et al. 2005). These literature values were either based primarily on data from aquatic consumers (VanderZanden and Rasmussen 2001; Post 2002) or specifically from salmonids (Trueman et al. 2005; McCutchan et al. 2013). We plotted consumer values against that of prey adjusted for each of the sets of TEF values separately to determine if consumer values were within the mixing polygon (Parnell et al. 2010). We ultimately chose values from Post (2002) (0.4 ± 1.3‰ for $\Delta\ \delta^{13}C$ and 3.4 ± 1.0‰ for $\Delta\ \delta^{15}N$) because the majority of plots evaluated showed that consumers fell within mixing polygons, whereas adjusting for TEF values from the other literature sources resulted in fewer plots where consumers were within mixing polygons.

To compare salmonid diets among macrohabitat types, seasons, and reaches, we ran unique diet models for each sampling event where fish were caught and organized the resulting estimates graphically in order to detect dietary patterns. While MixSIAR allows for up to two covariates and a nested design template, the current version does not simultaneously allow for multiple sets of informative priors to be defined for specific consumer groups; therefore, at the expense of further quantifying variation between consumer groups, we chose to run separate models for each consumer group in order to more specifically define informative priors from each group's stomach content data. If Chinook and Coho individuals were caught in the same sampling site, we pooled the two species in the diet model to simplify interpretation of large-scale diet patterns. Overall, mean $\delta^{13}C$ values of all freshwater invertebrate functional feeding groups (collectors, grazers, shredders, and predators) were not significantly different (Kruskal-Wallis H-test; $H = 5.23$, $p = 0.16$); therefore, we combined these functional feeding groups into a single "freshwater" invertebrate prey type for each sampling event for use in stable isotope mixing models. Terrestrial invertebrates were absent in a small number of the drift and benthic samples; in these cases, we used the pooled isotopic signatures of terrestrial prey from other sampling events within the same reach and season as a surrogate. We used the same marine source values for all models within a year, which included any salmon carcass and egg samples collected across the entire river. We report proportional contributions of each prey type as the mean of the posterior distributions with 2.5 and 97.5% lower and upper credible intervals. We verified that all models converged using Geweke's criterion and trace plots given from the MixSIAR model output (Stock and Semmens 2013).

2.4 Results

2.4.1 Freshwater invertebrate energy source contributions

Relatively strong correlations between freshwater invertebrate and periphyton $\delta^{13}C$ signatures suggested that invertebrate feeding groups relied primarily on freshwater, rather than terrestrial sources of carbon (Table 2.3, Fig. 2.2). For both 2013 and 2014, site-specific mean periphyton $\delta^{13}C$ predicted site-specific mean primary consumer $\delta^{13}C$ better than did terrestrial organic matter (OM) $\delta^{13}C$ for all freshwater primary consumer groups (Table 2.3). Multiple linear regressions for collector, grazer, and shredder invertebrate $\delta^{13}C$ against periphyton $\delta^{13}C$ in both years were significant ($p < 0.05$) and resulted in relatively high partial r^2 values (range: 0.597 to 0.869), whereas all relationships of invertebrate groups to terrestrial OM were not significant ($p > 0.05$) and had negative partial r^2 values (range: -0.245 to -0.037; Table 2.3). In 2013, associations of all primary producer invertebrate groups to periphyton were weaker (slopes deviating from 1 with lower partial r^2 values) than groups collected in 2014, suggesting a lower reliance on both carbon sources (Table 2.3, Fig. 2.2a-c). Collectors in 2013 appeared to be most reliant on periphyton, followed by shredders and finally by grazers (Table 2.3, Fig. 2.2a-c). In 2014, collectors again appeared to have the strongest reliance on periphyton, followed by grazers and shredders (Table 2.3, Fig. 2.2d-f).

2.4.2 Juvenile salmon diet

2.4.2.1 Stomach contents

Stomach content analysis revealed that while the diet composition of juvenile salmon varied across years, seasons, and macrohabitat types, freshwater prey were overall the most important. In 2013, 216 juvenile Chinook and Coho individuals were sampled for stomach

contents, however only stomach content samples from 161 individuals were able to be used for analysis after accounting for empty stomachs and those with entirely non-identifiable prey contents. Analysis revealed that freshwater prey dominated the diets (by mass) overall, followed by marine and terrestrial prey types (Table A-2, Fig. 2.3). The proportion of marine-derived prey items (salmon eggs) in stomachs increased from spring to fall and was highest in tributary mouths relative to other macrohabitat types (Table A-2, Fig. 2.3). Contributions of freshwater prey were generally greatest in spring and decreased through fall, whereas the importance of terrestrial prey stayed relatively constant across seasons (Table A-2, Fig. 2.3). Sampling efforts in 2014 yielded 277 non-empty and fully identifiable stomach content samples from a total of 316 juvenile Chinook and Coho individuals, collected across a larger number of sites than the previous year. In 2014, freshwater prey were more important in diets compared to 2013, complemented by a large decrease in the proportion of marine and terrestrial prey (Table A-2, Fig. 2.4). Stomach content samples pooled by season for 2014 again showed freshwater prey were marginally most important in spring and decreased during summer when terrestrial prey peaked in importance (Table A-2, Fig. 2.4). Marine-derived prey items were only found in diets at one sampling site during summer sampling events and were therefore negligible in overall diet composition for that season (Table A-2, Fig. 2.4). Overall importance in diets of salmon eggs in 2014 was highest in fall when salmon eggs made up a more substantial proportion of diets at several upland slough and side slough sites throughout the river (Table A-2, Fig. 2.4).

Diptera larvae and adults were the most prevalent invertebrate prey taxon by mass found in fish stomachs pooled across both years (21.5 and 15.3%, respectively; Table 2.4). Other important freshwater invertebrate taxa in fish stomachs were larval and adult Trichoptera, larval and adult Plecoptera, and larval Ephemeroptera (Table 2.4). The most prevalent terrestrial taxon

by mass was Hymenoptera, followed by Coleoptera, Lepidoptera, Hemiptera, and Diptera (Table 2.4).

2.4.2.2 Bayesian stable isotope diet modeling

Mixing model results suggested that juvenile salmon consumed primarily freshwater invertebrates during both years, while terrestrial invertebrates and salmon eggs were secondary prey items (Table A-3, Figs. 2.5, 2.6). MixSIAR diet models estimated that in 2013, freshwater prey contributed on average 46.2 ± 12.3% SD (range: 24.8 to 69.0%) to assimilated diets across all habitats and seasons (Fig. 2.5). Terrestrial and marine sources were still significant to diets but less important, representing mean contributions of 27.4 ± 11.9% SD (range: 14.9 to 43.3%) and 26.3 ± 9.6% SD (range: 3.0 to 54.7%), respectively. In 2014, freshwater prey comprised an even greater proportion of salmon diets (mean: 57.2 ± 13.1% SD; range: 24.9 to 79.0%) compared to the previous year, while terrestrial prey increased slightly (mean: 28.3 ± 12.5% SD; range: 8.4 to 66.2%), and marine-derived prey played a significantly reduced role (mean: 14.5 ± 8.6% SD; range: 2.5 to 40.3%). All models considered here showed evidence of convergence to posterior distributions according to Geweke's criterion and trace plots provided by mixing model diagnostics. Freshwater and terrestrial diet sources often overlapped to some extent in isotopic space, which contributed a mean Pearson's correlation coefficient of -0.78 (range: -0.32 to -0.97) between these two sources for all diet models pooled across both years.

a) Spatial variability

In 2013, the 95% credible intervals of each prey type, but especially freshwater and terrestrial prey, between the habitats sampled (upland sloughs, tributary mouths, and side

channel) generally had a high degree of overlap, suggesting only small differences (Table A-3, Fig. 2.5). The greatest contribution of marine sources occurred in tributary mouth sites where stomach content analysis indicated juvenile salmon fed most heavily on salmon eggs relative to other habitat types (Table A-3, Fig. 2.5). Macrohabitat types sampled in 2014 also showed significant overlap in the possible mean contributions of each prey source (Fig. 2.6), with notable exceptions in two upland slough habitats (Reaches 1 and 3) where spawning salmon were observed in relatively higher densities and a higher proportion of stomach contents contained salmon eggs (see stomach content results, Fig. 2.4). Diet composition by distance from the river mouth did not yield any consistent or significant trends in either year (box colors, Figs. 2.5, 2.6).

b) Seasonal variability

In 2013, the mean contributions of both freshwater and terrestrial prey sources decreased seasonally for fish caught in most of the sites sampled (Table A-3, Fig. 2.5). Contributions from marine prey conversely increased from spring to fall, most dramatically in tributary mouths where densities of spawning salmon were higher compared to upland sloughs and the side channel (Table A-3, Fig. 2.5). In 2014, contributions of each prey source among macrohabitat types showed less contrasting seasonal trends compared to the previous year (Table A-3, Fig. 2.6). Mixing model results for most sites revealed that the importance of freshwater prey in diets either decreased slightly from spring to fall or had the lowest overall contribution during the summer (Table A-3, Fig. 2.6). Terrestrial prey generally showed opposing seasonal trends relative to freshwater prey, in which mean contributions either increased from spring to fall or peaked in summer. These 2014 seasonal patterns were evident for fish populations caught in all macrohabitat types. Seasonal trends of marine contributions were highly variable among sites

sampled, however in sites where spawning salmon were observed in relatively higher densities (Reach 3 tributary mouth and upland slough; Reach 1 upland slough), the mean contribution of marine prey sources increased slightly from summer to fall (Table A-3, Fig. 2.6). Fish sampled in most sites showed a decrease in the mean contribution of marine sources from spring to summer (Table A-3, Fig. 2.6) in agreement with decreases in mean $\delta^{15}N$ ratios for fish in those sites (Table A-1).

2.5 Discussion

2.5.1 Freshwater invertebrate energy source contributions

Results from multiple linear regressions of freshwater invertebrate – source $\delta^{13}C$ showed that site-specific periphyton $\delta^{13}C$ predicted $\delta^{13}C$ for all functional feeding groups better than did terrestrial OM $\delta^{13}C$, suggesting that these primary consumers were predominantly assimilating instream sources of carbon. Interestingly, lower slope estimates and smaller partial r^2 values for 2013 regressions suggested weaker relationships between consumers and periphyton without complementary strong relationships between consumers and OM (Table 2.3, Fig. 2.2). The weak relationships for this year may be a function of relatively high flows and turbidity, when main channel discharge was overall higher than in 2014. These instream conditions may have reduced periphyton standing stocks and availability as a food source to invertebrates (Lloyd 1987) and promoted invertebrate dispersal from newly-connected habitats (Gibbins et al. 2007, 2010) where they assimilated the majority of their carbon, thereby decoupling site-specific invertebrate and periphyton $\delta^{13}C$ and contributing to an apparent low reliance on that food source. Other possible sources of variability in the associations between consumer and food source $\delta^{13}C$ that was observed for both years include within-site patchiness of $\delta^{13}C$ controls (e.g. velocity,

temperature, DIC source) that affect overall composite sample values and within-site variations in periphyton species assemblages (Zah et al. 2001).

Freshwater production is often the predominant carbon pathway in river food webs, and despite the prevalence of terrestrial OM, multiple invertebrate feeding groups have been known to rely on freshwater algae presumably because it is a more labile food source and has a higher nitrogen content (Junk et al. 1989; Sedell et al. 1989; Gaedke et al. 1996; Lewis et al. 2001). The relatively strong relationship between collector, grazer, and shredder functional feeding group $\delta^{13}C$ and periphyton $\delta^{13}C$ in the Susitna agrees with studies conducted in other glacial and non-glacial river systems that reported feeding plasticity and a general reliance on instream autotrophy by the same groups (Palmer et al. 1993; Miller et al. 1998; Zah et al. 2001).

2.5.2 Juvenile salmon diet patterns

Mixing model results suggested that freshwater invertebrate prey were the most important diet items for juvenile Chinook and Coho salmon overall (Table A-3, Figs. 2.5, 2.6). A relatively sparse dataset in 2013 precluded comparisons among all available sites; however, freshwater invertebrates were on average the primary diet item for this year (46.2%), with terrestrial and marine prey items also making up substantial mean contributions to diets (27.4 and 26.3%, respectively). Freshwater prey became more important to juvenile salmon diets in the following year (57.2%), and the role of marine prey was reduced (14.5%). This change was also reflected in the drastic decrease in salmon eggs enumerated in 2014 stomach content samples.

The interpretation and discussion of more detailed findings requires addressing a number of assumptions under which the diet models operated. Perhaps the greatest assumption is that juvenile fish were relatively immobile within their respective sites of capture, and were feeding

there long enough to reach isotopic equilibrium with the local prey. At least a subset of fish likely obtained their isotopic signatures while feeding in other habitats, especially given that some samples were obtained from smolting juveniles that could have already migrated long distances from upstream reaches. For this and other reasons, applying stable isotope methods to migratory stream fishes is complex (Doucett et al. 1996; Perry et al. 2003). Despite this caveat, stable isotope evidence suggests that juvenile salmon in the Susitna River maintained consistent rearing populations long enough to represent distinct, local isotopic signatures by the summer sampling event. A juxtaposition of salmon and invertebrate $\delta^{15}N$ and $\delta^{13}C$ values from distinct habitats with those of the respective local invertebrate prey shows that during the summer sampling event (mid-August; Fig. 2.7b), fish collected within macrohabitats at Reach 2 were presumably at isotopic equilibrium with the local prey, including those found within the margins of the glacial main and side channel. Murphy et al. (1989) also observed juvenile Chinook Salmon, and Coho Salmon to a lesser extent, utilizing the margins and braids of the glacial main channel in the Taku River, Alaska. This stable isotope data corroborates their findings and provides evidence that both juvenile Chinook and Coho salmon in the Middle Susitna forage on local invertebrate prey found within glacial habitats.

The $\delta^{15}N$ vs. $\delta^{13}C$ plot for the spring sampling event (mid-June; Fig. 2.7a) indicates less defined populations relative to those sampled in summer, which could be explained by recent immigration to these habitats and therefore tissues that are not yet at isotopic equilibrium (Bradford et al. 2001; Perry et al. 2003). The fall (late-September) plot shows that site-specific salmon and invertebrate signatures were still somewhat separated in isotopic space but with greater spread and overlap than the summer sampling event. This greater spread of consumer isotope signatures possibly represents recent mixing across space or differential growth rates

among individual fish (Fig. 2.7c). These interpretations align with observations of juvenile Chinook Salmon movement within the glacially-influenced upper Yukon River (Bradford et al. 2001) which were observed moving downstream from their natal spawning grounds or overwintering areas, colonizing new habitats from May through July where they reared for the rest of the summer.

Credible intervals around mean freshwater and terrestrial source contributions in particular were large and therefore precluded more definitive diet assignments (Table A-2, Figs. 2.5, 2.6). Robust interpretation of stable isotope diet models requires isotope values of diet sources to be distinct enough in order to differentiate their importance in consumer diets (Moore and Semmens 2008); however, freshwater and terrestrial sources overlapped to some extent within a number of sites, with correlations between posterior estimates of these two sources ranging between r = -0.39 to -0.97. In cases where sources were highly correlated and the model was unable to discern source contributions from isotope data, prior information from stomach content data were more influential in guiding proportional contribution estimates (Moore and Semmens 2008). Many of the terrestrial and freshwater diet estimates with large credible intervals correspond to glacial main and side channels, where the overall difference in mean $\delta^{13}C$ between freshwater and terrestrial invertebrates was smallest relative to differences in other macrohabitat types (difference of means: 1.3 and 1.2‰ respectively; Table A-1, Fig. 2.6). Terrestrial invertebrate $\delta^{13}C$ was more variable than expected (range across all $\delta^{13}C$ values: -35.72 to -22.76‰) and often exhibited the same site-specific isotopic shifts as freshwater invertebrates, namely ^{13}C-enriched values at glacial habitats relative to off-channel habitats (Table A-1, Fig. 2.7). One potential explanation for this pattern is a reciprocal flow of carbon from freshwater to terrestrial habitats via consumption of local emerging aquatic insects by

predatory terrestrial spiders and beetles (Power and Rainey 2000; Collier et al. 2002; Paetzold et al. 2006).

2.5.2.1 Spatial variability

Taking these factors into account, comparisons of diet model results across macrohabitats (Figs. 2.5, 2.6) show that there was generally a high degree of overlap between model estimates for fish diets among different macrohabitat types. Both freshwater and terrestrial prey comprised similar proportions in diets across the heterogeneous macrohabitats sampled, except where salmon eggs made up a significant proportion of diets. Despite relatively high turbidity, the freshwater pathway was the predominant source for juvenile salmon rearing in glacial main and side channel habitats in 2014 (range in mean freshwater contribution: 40.0 – 79.0%; Table A-3, Fig. 2.6). This finding contrasts with the that made by Perry et al. 2003, where juvenile salmon rearing in turbid habitats above 10 NTU (Nephalometric Turbidity Units) did not assimilate any autochthonous prey sources, however their study was conducted in an unglaciated catchment with recent fire disturbance. An increase of suspended solids on biota in these typically undisturbed streams may therefore be relatively more detrimental than for those adapted to living in glacial habitats. In 2013, salmon eggs were consumed in all macrohabitat types sampled (upland slough, tributary mouth, and side channel), however tributary mouths were the most important sites for egg consumption (Figs. 2.3, 2.5). In 2014, egg consumption in tributary mouths was reduced compared to the previous year, and conversely was higher in upland sloughs and the side slough site (Figs. 2.4, 2.6). No stomach content evidence exists to suggest that juvenile salmon consumed salmon eggs during any sampling period in glacial-fed main channel habitats (Figs. 2.3, 2.4), but salmon eggs were presumably consumed to some extent within the

glacial-fed side channel in Reach 2 (Fig. 2.4). Telemetry surveys of spawning salmon in the Susitna River in 2013 confirmed that tributary mouths were the most heavily used spawning locations, and to lesser extents, slough and side channel habitats (LGL Alaska Research Associates and ADF&G 2014). Potential spawning behavior was observed at main channel margins, however no nest digging was confirmed due to high turbidity (LGL Alaska Research Associates and ADF&G 2014). The heavy use of tributary mouths by spawning salmon in 2013 parallels consumption of salmon eggs by juvenile salmon in this macrohabitat type, and suggest that in the Susitna, tributary mouths in particular can be important hotspots of high quality marine prey pulses to rearing salmon.

No consistent or discernable diet pattern was observed relating to distance from the river mouth (Figs. 2.5, 2.6). Mixing model means and credible intervals grouped by macrohabitat type and season from among all reaches generally overlapped to such an extent as to suggest that no strong upstream to downstream trend in food source contributions existed, and potentially obscured a more definitive trend that would have been apparent with less error around mean estimates (Figs. 2.5, 2.6). The combination of seasonal and environmental drivers acting on instream production and on the input of subsidized material within individual sites of the same habitat classification are likely distinct enough to produce diet patterns that are inconsistent with a longitudinal effect (Poole 2002, Stanford et al. 2005). For example, while juvenile salmon rearing in all sampled tributary mouths in 2013 were supported by marine-derived food, the direction and magnitude of those contributions varied over time between tributary mouth sites (Fig. 2.5). This resulting effect likely depends on a large range of possible factors such as non-overlapping spawning habitat preferences and run timing between different species of adult salmon (Wipfli and Baxter 2010; LGL and ADF&G 2014). In contrast to findings from this

study, contributions to juvenile Atlantic Salmon inhabiting a river system in New Brunswick, Canada showed a longitudinal effect consistent with the river continuum concept (Vannote et al. 1980), where fishes received the highest proportional contribution of terrestrial carbon in smaller headwaters with extensive canopy cover and continually less in open, downstream reaches (Doucett et al.1996). We might have seen a similar longitudinal effect if our study reaches extended from the headwaters and lower order streams to the river mouth; however, all of our sampling sites were located adjacent to the main channel in a 169-km stretch of the middle river.

2.5.2.2 Seasonal variability

Mixing models estimated that freshwater prey contributions remained substantial during all seasons at most sampling sites, and often either decreased in importance from spring to fall (Fig. 2.5) or were least important during the summer sampling period (mid- to late-August) when terrestrial prey were often most important to diets (Fig. 2.6). A review of studies documenting consumption of terrestrial invertebrates by stream fishes reveals that temporal patterns are highly variable by year and system (Baxter et al. 2005); however, a common pattern in higher latitude river systems is an increase in the flux of terrestrial invertebrates to streams during mid-summer when terrestrial productivity can be at its highest and when invertebrates are most active (Chloe and Garman 1996; Wipfli 1997; Bridcut 2000; Nakano and Murakami 2001; Gutierrez 2011). Because salmonids are opportunistic predators and are known to selectively forage for terrestrial invertebrates (Hubert and Rhodes 1989; Young et al. 1997; Nakano et al. 1999), a large-scale pulse of this prey subsidy during mid-summer may account for increased contributions to these fish populations. While this pattern seemed to be evident and widespread for fish sampled across all macrohabitat types in 2014 (Fig. 2.6), terrestrial contributions for fish in 2013 generally

decreased from spring to fall (Fig. 2.5). A drastic increase in the consumption of salmon eggs from spring to fall for this year (Fig. 2.5) may be masking a similar mid-summer peak in terrestrial prey, since salmon eggs are a higher quality food resource (Quinn et al. 2012) and are known to be a preferred prey source when available in the environment (Bilby et al. 1998).

Interestingly, 2014 mixing models for sampling sites where no eggs were found in diets often exhibited peaks in marine contributions in spring followed by a decrease in summer and more variable contributions in fall (Fig. 2.6). Strong influence from the stable isotope data may explain the higher marine contribution observed in the spring despite the lack of eggs in stomach contents; indeed, mean fish $\delta^{15}N$ was significantly higher during spring sampling events (8.2 ± 1.6‰ SD) relative to summer (6.8 ± 1.2‰ SD; $H = 50.2$, $p < 0.001$). For year-0 individuals, higher $\delta^{15}N$ values earlier in the year may be explained by consumption of recently emerged salmon fry that contain residual maternal marine signatures (Doucett et al. 1999). For age-1 individuals with slower tissue turnover, it is more likely that a higher $\delta^{15}N$ value early in the growing season is attributed to over-winter storage of marine-derived nitrogen that was assimilated in tissues the previous fall when salmon eggs were consumed. This effect was observed for stream-resident Dolly Varden in Southcentral Alaska, where evidence from stable isotopes and fatty acid analysis suggested that marine-derived nutrients persisted in tissues for at least nine months after feeding on salmon eggs the previous summer, possibly due to low winter energetic demands that slow tissue turnover (Rinella et al. 2013). Given the disparity between stomach content and stable isotope evidence of marine dietary influence and the number of potential mechanisms explaining seasonal variability in $\delta^{15}N$, small seasonal differences in marine dietary contributions estimated by models should be interpreted cautiously.

Overall, this study demonstrates that the freshwater energy pathway was most important to aquatic invertebrate primary consumers as well as juvenile Chinook and Coho salmon rearing in diverse macrohabitats throughout the middle Susitna River. Marine and terrestrial prey both comprised substantial portions of juvenile salmon diets at certain locations and periods throughout the growing season and likely reflected varying availability of these food subsidies. While previous studies have observed the utilization of multiple energy pathways by juvenile salmon, it is rare to find information on the importance of these pathways throughout the habitat mosaic and across seasons in river networks. This study provides spatial and temporal context for the variable trophic relationships between juvenile salmon and multiple prey sources, and suggests widespread food resource pulses across the landscape, such as a potential flux of terrestrial invertebrates during mid-summer.

This study provides an assessment of baseline trophic conditions for rearing salmon below the potential site of a large hydroelectric dam. Because dam operations will likely affect seasonal hydrological regimes that in turn influence habitat quality as well as the distribution and availability of food sources for stream fishes (Vinson 2001; Young et al. 2011; Holt et al. 2014), these results can be used by dam operators to monitor post-construction conditions and can help to predict and mitigate for negative impacts on a large scale. Future investigations are needed to improve the applicability of this study and other salmonid diet studies across heterogeneous river systems. To appreciate how variable diet patterns contribute to growth and production of salmonids throughout a diverse river system, studies should incorporate a growth modeling component that takes all major food sources (e.g. relative availabilities, nutritional qualities, energy densities) and environmental conditions that affect physiology into account. While the latest diet modeling tools can simultaneously consider both stomach content and stable isotope

data, other considerations (e.g. concentration of essential nutrients; fat content; availability of high quality food relative to other sources, life history shifts, and body condition) will help to shape a more holistic understanding of the importance of various food resources to consumers. Such information, in conjunction with results from this study, can provide a basis for understanding food-driven limitations to the productivity of Pacific salmon populations at the freshwater rearing stage.

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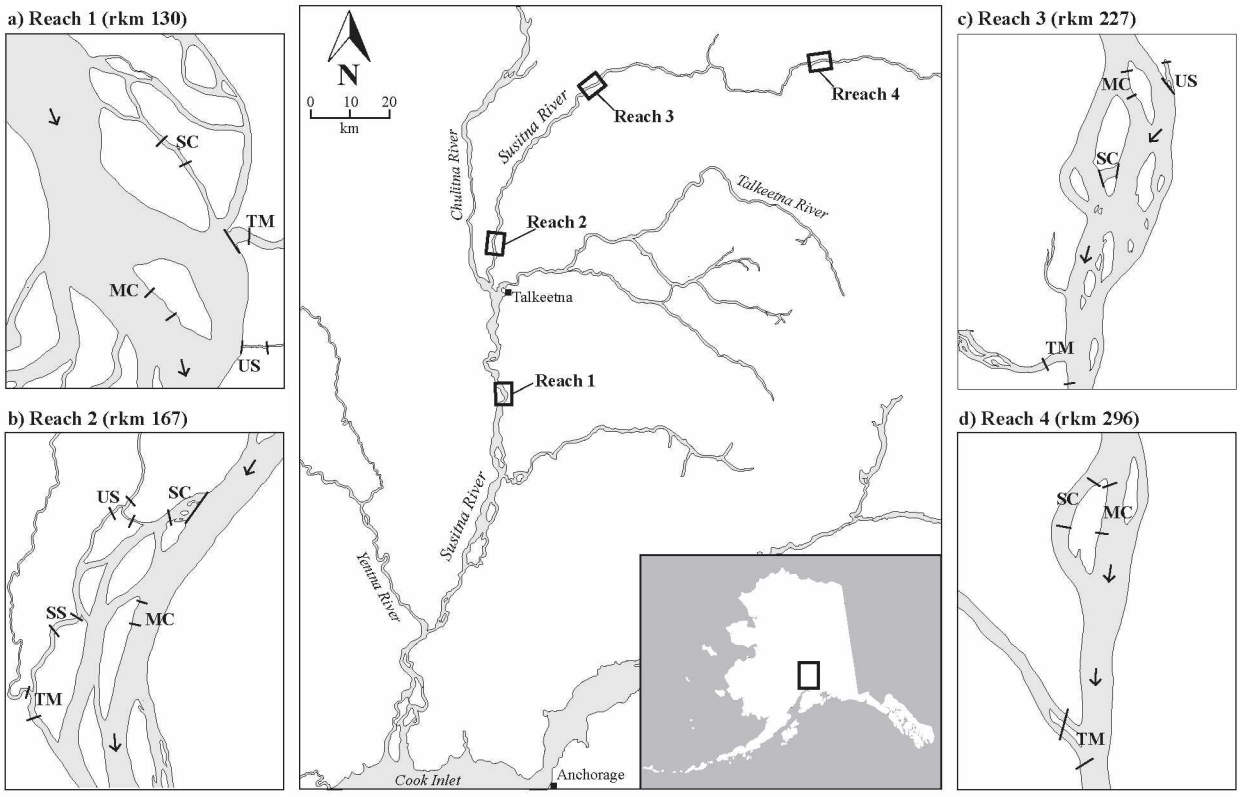

Figure 2.1 Study area showing the upper and lower extents of each sampling site, identified by macrohabitat type (TM: tributary mouth, SS: side slough, US: upland slough, SC: side channel, MC: main channel) within study reaches 1-4 (panels a-d). Arrows indicate direction of flow.

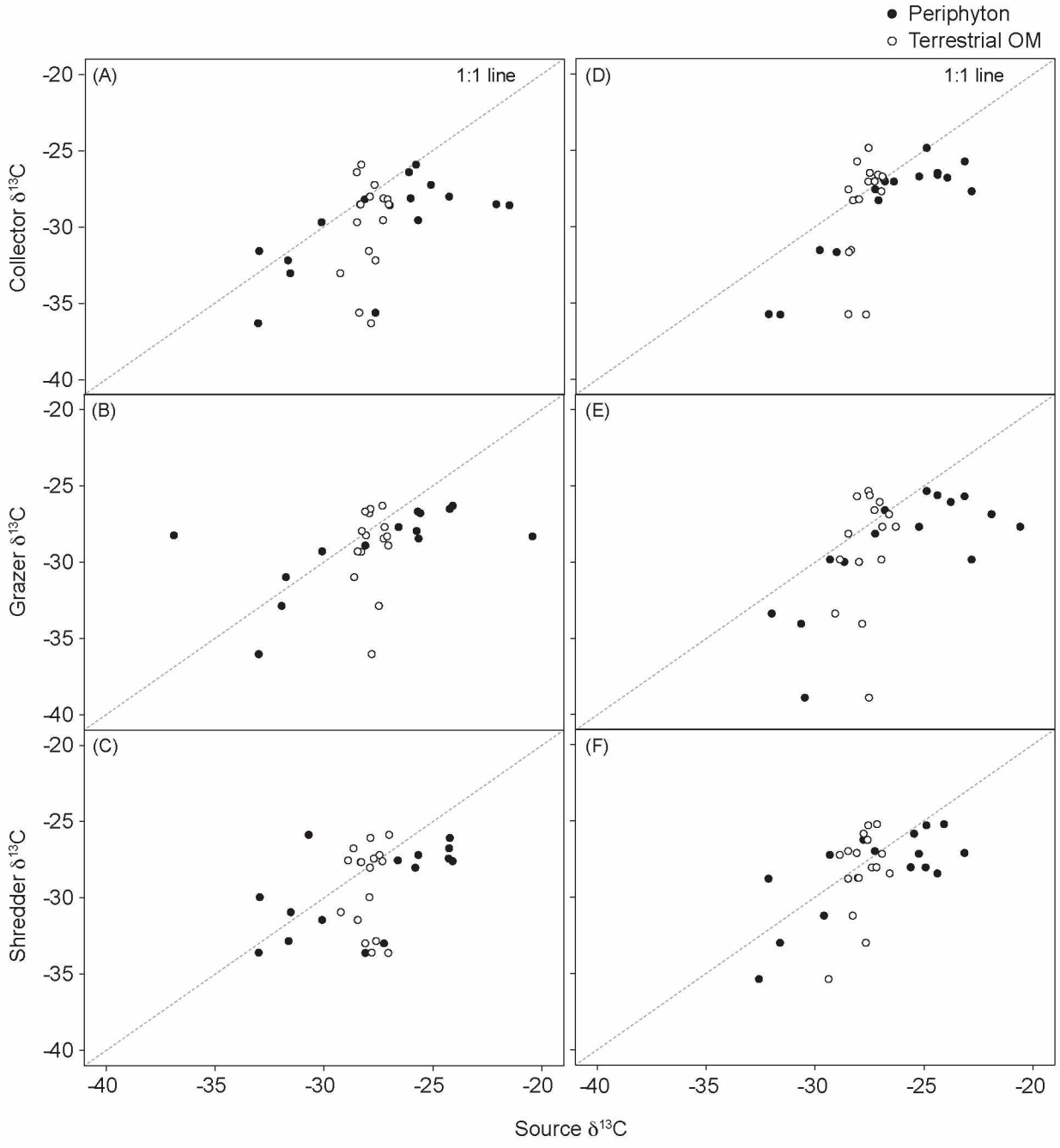

Figure 2.2 Relationships of aquatic invertebrate consumer group $\delta^{13}C$ with potential food source (periphyton [filled circles] and terrestrial organic matter [open circles]) $\delta^{13}C$ for 2013 (panels A – C) and 2014 (panels D – F). Each data point represents site-specific mean invertebrate $\delta^{13}C$ vs. site-specific mean source $\delta^{13}C$ for all seasons combined.

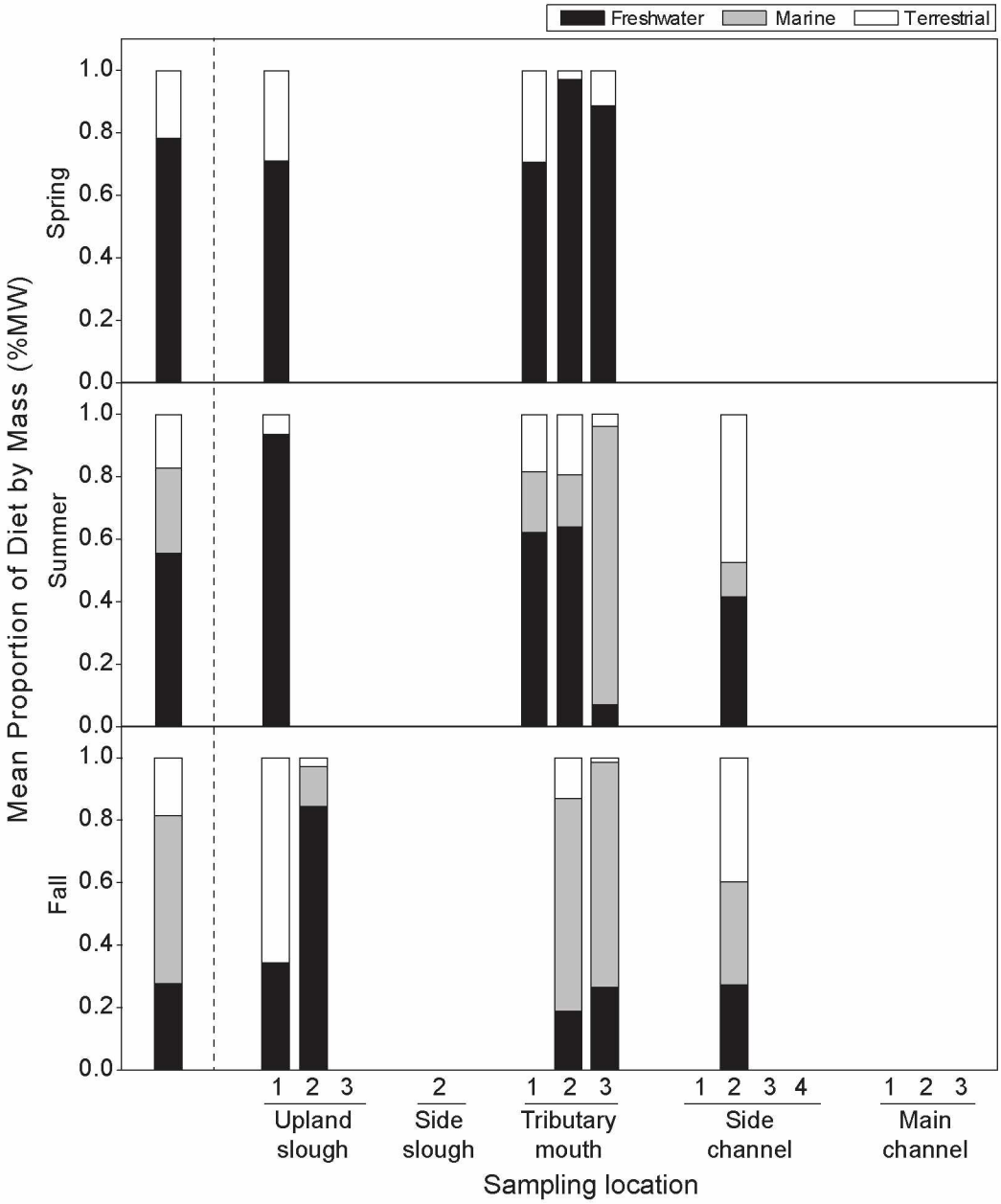

Figure 2.3. Mean proportion by mass of freshwater, marine, and terrestrial prey categories in the stomachs of juvenile Chinook and Coho salmon collected at each sampling location in spring, summer, and fall of 2013. Numbers grouped by macrohabitat type indicate relative reach locations, where increasing number corresponds to increasing distance from the river mouth. The separated bar on the far left represents the diet composition for all stomach samples collected in that season.

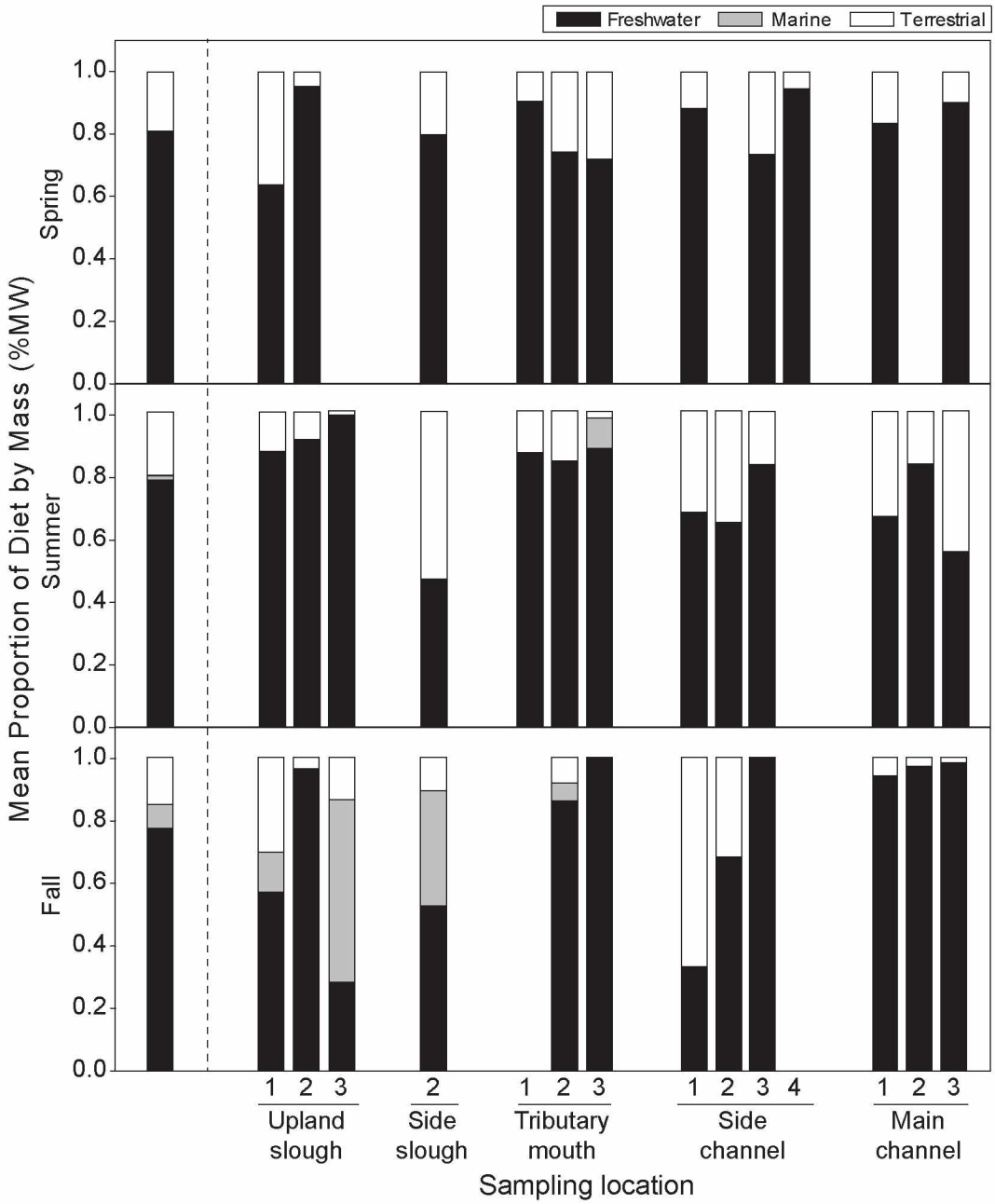

Figure 2.4. Mean proportion by mass of freshwater, marine, and terrestrial prey categories in the stomachs of juvenile Chinook and Coho salmon collected at each sampling location in spring, summer, and fall of 2014. Numbers grouped by macrohabitat type indicate relative reach locations, where increasing numbers corresponds to increasing distances from the river mouth. The separated bar on the far left represents the diet composition for all stomach samples collected in that season.

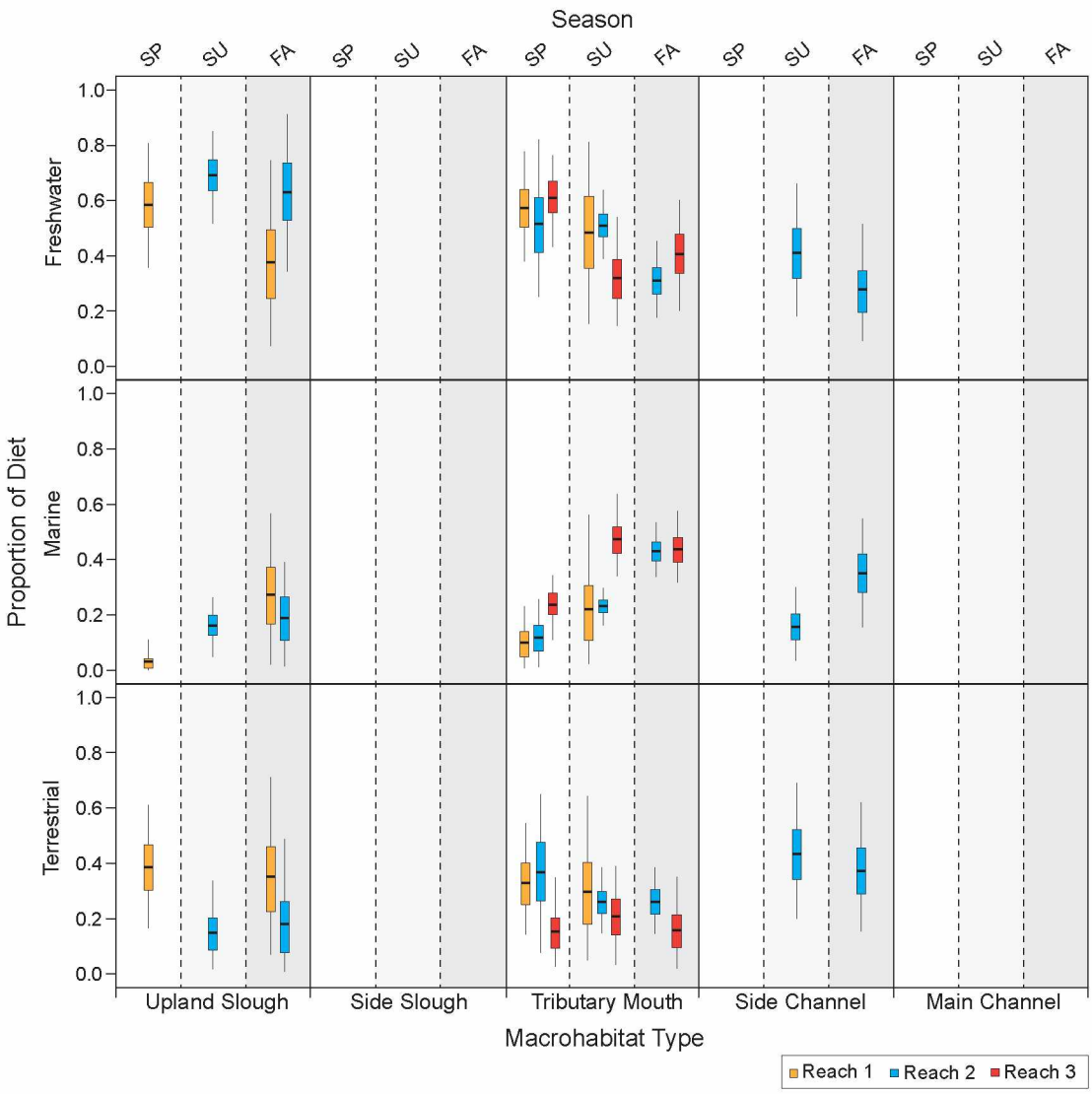

Figure 2.5. Diet composition of juvenile salmon in 2013, as estimated with MixSIAR Bayesian mixing models. Boxplots show the mean proportional contribution (with 2.5, 25, 75, and 97.5 credibility intervals) of each prey category to the overall diet. Contributions of all diet sources from a single sampling event are stacked vertically across panels. Model results are grouped so that all spatial and temporal dietary trends addressed in this study may be discerned: first by macrohabitat as indicated by labels at the bottom of the plot, then by season as indicated by panel color and labels at the top of the plot (SP = spring, SU = summer, FA = fall), and lastly by increasing distance from the river mouth as indicated by box color (see legend).

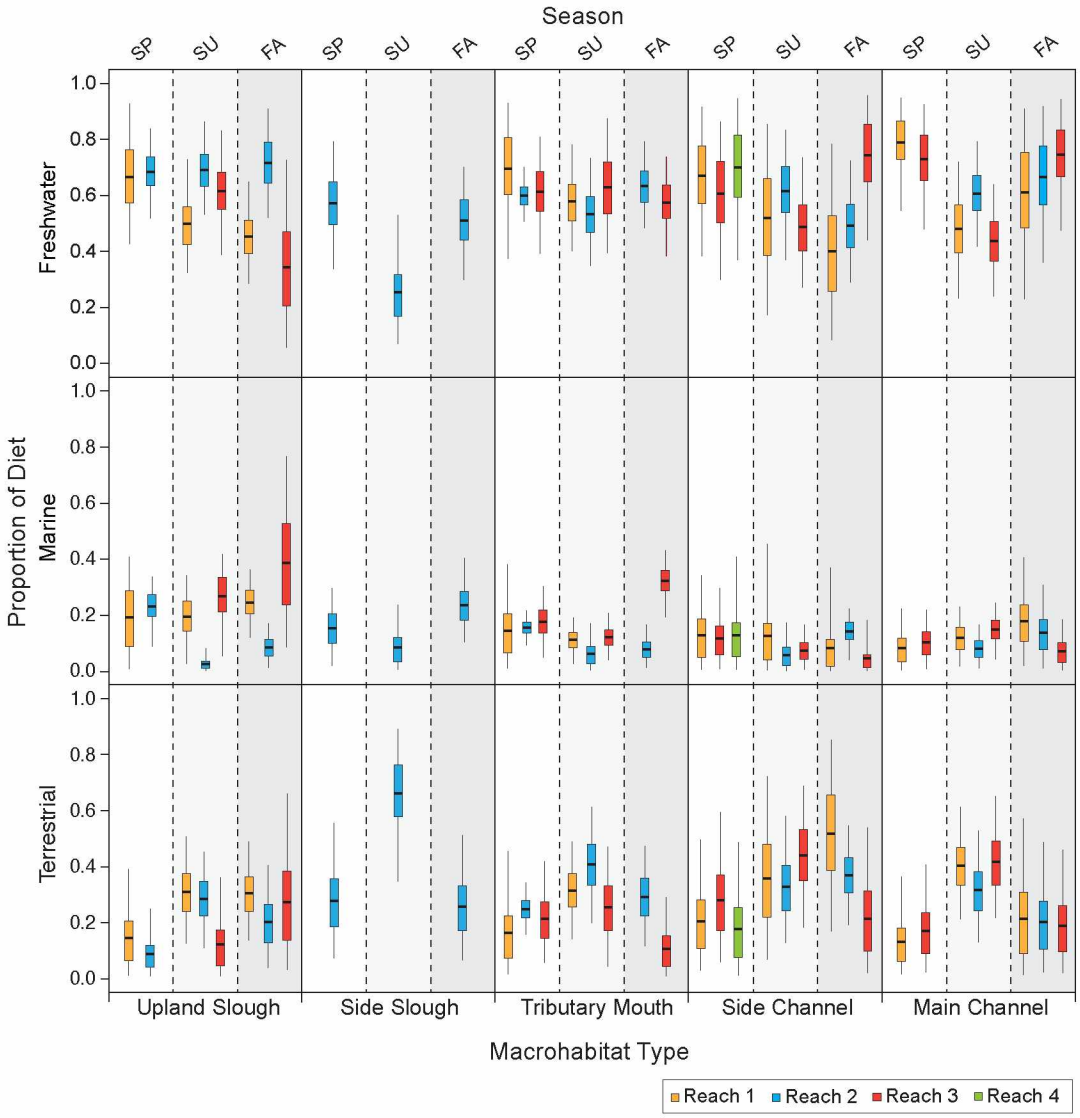

Figure 2.6. Diet composition of juvenile salmon in 2014, as estimated with MixSIAR Bayesian mixing models. Boxplots show the mean proportional contribution (with 2.5, 25, 75, and 97.5 credibility intervals) of each prey category to the overall diet. Contributions of all diet sources from a single sampling event are stacked vertically across panels. Model results are grouped so that all spatial and temporal dietary trends addressed in this study may be discerned: first by macrohabitat as indicated by labels at the bottom of the plot, then by season as indicated by panel color and labels at the top of the plot (SP = spring, SU = summer, FA = fall), and lastly by increasing distance from the river mouth as indicated by box color (see legend).

Figure 2.7. $\delta^{15}N$ and $\delta^{13}C$ values for juvenile Chinook and Coho salmon (open symbols, representing individuals) and their potential prey items (closed circles; means ± 1 SD) separated by macrohabitat within Reach 2 (rkm 167) during the a) spring, b) summer, and c) fall sampling events. Colors of fish and invertebrate symbols indicate habitat types. The isotopic signatures of marine-derived prey (salmon eggs and carcasses) were pooled across all habitat types (black circles with dashed error bars). Freshwater sources are indicated by solid error bars and terrestrial sources by dotted error bars.

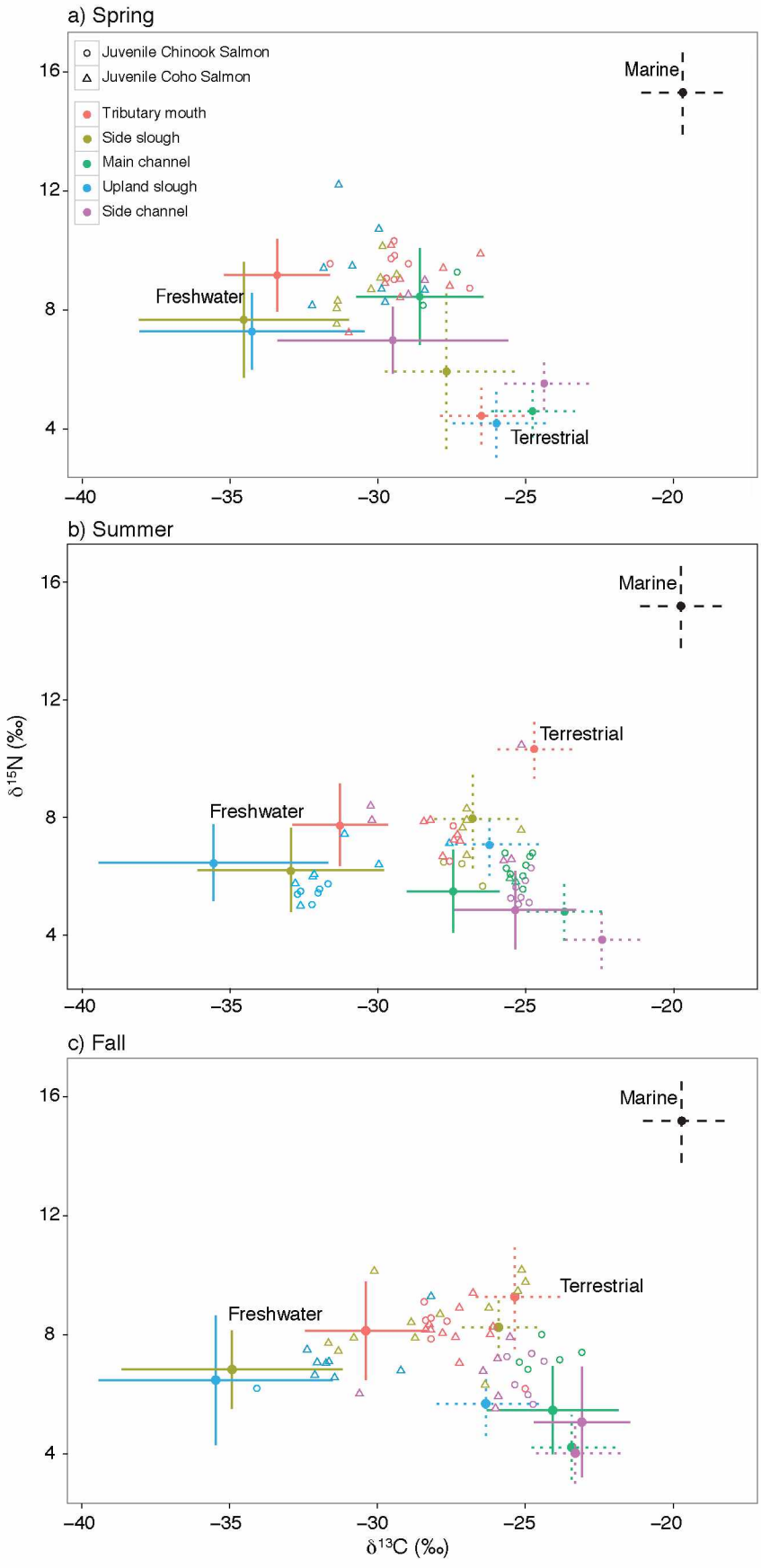
a) Spring
Juvenile Chinook Salmon
Juvenile Coho Salmon
Tributary mouth
Side slough
Main channel
Upland slough
Side channel
Marine
Freshwater
Terrestrial
b) Summer
Marine
Terrestrial
Freshwater
c) Fall
Marine
Terrestrial
Freshwater
δ15N (‰)
δ13C (‰)
16
12
8
4
−40
−35
−30
−25
−20

Table 2.1 Key characteristics of macrohabitat types sampled.

Macrohabitat Type (code)	Description					
	Connectivity to main channel	Water source	Relative turbidity	Mean (range) water velocity ($m\ s^{-1}$)	Mean (range) water temperature (°C)	Typical spawning salmon activity
Upland slough (US)	Disconnected at upstream end; typical backwater connection at downstream end	Substantial contribution of clear water from tributaries or from upwelling groundwater; glacial backwater dependent on glacial main or side channel flows	Low to moderate	0.1 (0.0 – 0.6)	7.8 (2.8 – 11.0)	Reach 1: milling, no redds observed Reach 2: None Reach 3: milling, holding; redds and eggs observed
Side slough (SS)	Intermittently connected at upstream end; backwater connection at downstream end	Substantial contribution of clear water from tributaries or from upwelling groundwater; glacial backwater or upstream contribution dependent on glacial main or side channel flows	Low to moderate	0.2 (0.0 – 0.9)	5.6 (1.0 – 8.0)	Reach 2: milling, holding; few redds observed
Tributary mouth (TM)	Full	Primary contribution of clear water from tributary flows, influence of glacial main channel, side channel, or slough at downstream end	Low	0.5 (0.2 – 1.5)	8.0 (3.0 – 14.0)	Reach 1: milling, holding; few redds observed Reach 2: milling, holding; few redds observed Reach 3: many have been observed holding; redds and eggs observed
Main channel (MC)	-	Primarily glacial	Moderate to high	0.46 (0.1 – 1.3)	8.9 (2.5 – 14.0)	No observations
Side channel (SC)	Fully connected at upstream end except during periods of extreme low flows	Primarily glacial	Moderate to high	0.4 (0.1 – 1.3)	8.7 (2.0 – 13.0)	No observations

Table 2.2 Dates for spring, summer, and fall sampling events in 2013 and 2014.

	Sampling Period		
Year	Spring	Summer	Fall
2013	Jun 11 – Jul 13	Aug 12 – Aug 21	Sept 22 – Oct 2
2014	Jun 10 – Jun 20	Aug 4 – Aug 14	Sept 20 – Sept 30

Table 2.3 Results of multiple linear regressions for freshwater invertebrate consumer groups and potential carbon sources (periphyton and terrestrial OM). "r_{PT}" and "r_{OM}" represent partial correlation values of periphyton and terrestrial OM $\delta^{13}C$, respectively, and consumer group $\delta^{13}C$. This value shows the degree of association between either periphyton or terrestrial OM and the consumer group after removing the effects of the other carbon source.

		Whole	Periphyton			Terrestrial OM		
Year	Consumer group	model r^2	Slope estimate	P	r_{PT}	Slope estimate	P	r_{OM}
2013	Collector	0.339	0.591	0.013	0.623	-0.412	0.726	-0.099
	Grazer	0.287	0.422	0.018	0.619	-0.925	0.478	-0.207
	Shredder	0.258	0.518	0.019	0.597	-0.132	0.896	-0.037
2014	Collector	0.783	1.142	< 0.001	0.869	-0.802	0.378	-0.245
	Grazer	0.604	1.242	0.001	0.790	-2.603	0.053	-0.526
	Shredder	0.483	0.734	0.008	0.655	-0.339	0.730	-0.097

Table 2.4 Overall percent composition of freshwater and terrestrial invertebrate mass ingested by juvenile Chinook and Coho salmon.

Taxon, life stage	%
Aquatic	
Diptera, immature	21.5
Diptera, adult	15.3
Trichoptera, adult	12.7
Plecoptera, immature	9.4
Ephemeroptera, immature	9.3
Trichoptera, immature	3.8
Plecoptera, adult	1.6
Other	2.4
Terrestrial	
Hymenoptera, adult	6.0
Coleoptera, adult	4.1
Lepidoptera, all stages	2.0
Hemiptera, adult	1.8
Diptera, adult	0.1
Other	0.8
Unknown	9.2

3. General Conclusion

Juvenile Chinook and Coho salmon in the middle Susitna River were largely supported by freshwater primary production, and secondarily by marine and terrestrial prey subsidies, according to a series of broad-scale stable isotope analyses of multiple trophic levels. My data showed that freshwater invertebrate primary consumers were more reliant on freshwater periphyton than on terrestrial OM, and that these invertebrates were in turn the overall dominant prey of juvenile Chinook and Coho salmon. These findings follow other reports that instream autotrophy is the predominant carbon pathway in river food webs (Junk et al. 1989; Sedell et al. 1989; Lewis et al. 2001). More specifically, my findings corroborate those from other studies of juvenile salmonid diets in both glacial and non-glacial river systems in Alaska, that freshwater invertebrates were the predominant prey items (Loftus and Lenon 1977; Hansen and Richards 1985; Sagar and Glova 1987; Gutierrez 2011).

While the freshwater energy pathway was overall most important to juvenile salmon, terrestrial invertebrate prey also made up substantial portions of diets regardless of the macrohabitat type where fish were found or their position along the river corridor. While mixing model credible intervals were large, there was evidence that terrestrial prey were slightly more important during mid-summer for most populations. Peaks in terrestrial invertebrate infall from adjacent riparian habitats have been observed in several other studies conducted in temperate and subarctic streams (Wipfli 1997; Nakano and Murakami 2001; Baxter et al. 2005; Gutierrez et al. 2011), presumably because terrestrial productivity is highest during this period. Furthermore, our study shows evidence that the importance of marine-derived food resources for juvenile salmon is generally highest in the fall in certain tributary and slough habitats. Taken together, evidence from diet models supports the notion that the importance of different prey sources for stream

fishes is asynchronous, which may contribute to sustaining salmonids throughout the growing season when the availability of any one food source may be insufficient (Wipfli and Baxter 2010). Our stable isotope data also suggested that juvenile Chinook and Coho salmon generally foraged in distinct habitats, including glacially-influenced main and side channel habitats, for long enough to acquire isotopic signatures of the local prey. In conjunction with detailed PIT array studies that can track movement on finer scales, stable isotope analysis has potential to confirm particular locations within a reach as distinct foraging areas.

The overall objective of this study was to observe how major energy pathways that contribute to juvenile Chinook and Coho salmon vary at relatively large spatial and temporal scales. At this broad scope it can be difficult to detect the most important underlying effects that produce any one ecological pattern. This is true even more so in large, glacial river systems where consumer movement is well concealed and where the highly diverse physical landscape interacts with extreme seasonal variation to produce food webs that are constantly in flux and that interact over large distances. Coupled with large-scale, quantitative investigations of the availability of local freshwater prey as well as terrestrial and marine-derived subsidies, further questions regarding mechanisms underlying food web patterns may be answered. While constraints in stable isotope methods (e.g. differences in tissue turnover time among trophic levels, variable prey-consumer fractionation, isotopically similar prey sources) can limit the interpretability of results, it still remains as one of the best tools for tracing energy flow in biophysically complex ecosystems. By applying stable isotope analysis at large scales, the results from this study provide an understanding of background levels of food resource use by juvenile salmonids across a highly complex and seasonally dynamic landscape that has previously been lacking. In addition, hotspots throughout space and time where terrestrial and marine prey

subsidies contribute beyond background levels (e.g. tributary mouths) can be identified, whereas their relative importance may have gone unnoticed in studies operating at smaller scales. Attempts to further the understanding and applicability of riverine food web research should consider this variability that is inherent in food webs and environmental processes across diverse riverine landscapes.

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APPENDIX A

A-1. Mean stable isotope signatures (± SD) for all sample types collected. Reach number increases with distance from the mouth of the Susitna River.

Year	Reach	Habitat Type	Sample Type	Season								
				Spring			Summer			Fall		
				$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*	$\delta^{13}C$	$\delta^{15}N$	*n*
2013	1	US	PERI	-32.7 ± 0.7	-1.5 ± 1.4	3	-31.0 ± 0.7	-3.3 ± 4.5	3	-30.6 ± 0.9	1.3 ± 1.2	3
			OMS	-28.1 ± 0.8	1.3 ± 4.0	2	-30.4 ± 0.1	0.5 ± 0.3	2	-28.9 ± 0.0	-4.8 ± 2.4	2
			OMB	-30.7 ± 0.0	-0.8 ± 1.5	3	-28.5 ± 1.2	-3.3 ± 1.0	3	-30.0 ± 0.2	-6.2 ± 2.5	3
			A-INV	-32.1 ± 3.4	4.8 ± 1.6	8	-33.2 ± 2.0	4.1 ± 1.2	9	-30.8 ± 6.2	2.9 ± 2.9	8
			Coll	-33.3 ± 0.4	4.7 ± 1.6	3	-34.9 ± 2.3	4.8 ± 0.7	3	-30.8 ± 8.1	1.7 ± 3.6	4
			Graz	-29.3	2.6	1	-	-	-	-32.7 ± 7.4	4.7 ± 2.2	2
			Shred	-31.9	4.0	1	-32.4 ± 0.7	3.7 ± 2.1	3	-28.5	3.1	1
			T-INV	-29.9 ± 1.1		2	-24.9 ± 0.5	3.2 ± 0.7	2	-31.7 ± 6.0	1.2 ± 2.9	4
			CARC	-	-	-	-20.5	10.4	1	-	-	-
			EGG	-	-	-	-	-	-	-	-	-
			CHIN	-26.3 ± 2.3	6.9 ± 0.8	6	-	-	-	-	-	-
			COHO	-28.8 ± 2.1	7.8 ± 0.3	8	-	-	-	-26.1 ± 1.5	8.4 ± 1.6	5
		TM	PERI	-29.4 ± 1.8	1.6 ± 1.5	3	-29.7 ± 1.7	6.5 ± 2.9	3	-31.0 ± 1.9	3.7 ± 0.3	3
			OMS	-27.8 ± 1.1	-1.8 ± 0.2	2	-28.8 ± 0.4	0.7 ± 1.7	2	-28.5 ± 0.6	-4.5 ± 3.2	2
			OMB	-28.8 ± 0.0	-2.1 ± 0.4	3	-28.9 ± 0.1	-1.6 ± 1.2	3	-28.6 ± 1.4	-1.9 ± 0.6	3
			A-INV	-31.6 ± 4.3	3.6 ± 1.1	9	-30.6 ± 1.8	4.9 ± 1.4	9	-28.3 ± 1.6	4.6 ± 1.4	1
			Coll	-29.6 ± 0.5	2.9 ± 0.8	3	-30.8 ± 3.0	4.2 ± 2.2	3	-28.6 ± 0.6	4.9 ± 0.5	3
			Graz	-30.2 ± 2.2	4.7 ± 0.3	3	-30.6 ± 1.5	5.0 ± 1.3	2	-27.1 ± 1.8	5.0 ± 2.1	3
			Shred	-34.9 ± 6.8	3.1 ± 1.2	3	-31.644	4.31	1	-27.8 ± 0.4	4.4 ± 2.1	3
			T-INV	-	-	-	-25.5 ± 1.9	4.5 ± 1.7	3	-	-	-
			CARC	-	-	-	-19.9 ± 0.3	10.0 ± 0.6	4	-	-	-
			EGG	-	-	-	-	-	-	-	-	-
			CHIN	-26.2 ± 0.5	7.7 ± 0.8	7	-24.1	8.2	1	-	-	-
			COHO	-27.2 ± 2.3	9.2 ± 1.6	10	-27.9 ± 3.3	9.1 ± 1.7	3	-26.7 ± 1.9	9.0 ± 0.3	2
	2	US	PERI	-28.3 ± 0.6	2.1 ± 0.8	3	-24.6 ± 6.1	-2.6 ± 2.0	3	-29.7 ± 1.5	-0. ± 0.4	3
			OMS	-28.8 ± 2.2	0.3 ± 0.7	2	-28.7 ± 0.3	-0.2 ± 0.8	2	-27.4 ± 0.2	-0.6 ± 1.6	2
			OMB	-28.5 ± 0.4	-1.0 ± 1.1	3	-25.3 ± 3.8	-2.9 ± 1.4	3	-26.4 ± 0.5	-2.2 ± 0.2	3
			A-INV	-35.6 ± 3.2	3.9 ± 1.1	5	-34.0 ± 1.8	2.7 ± 1.2	10	-31.8 ± 4.8	1.4 ± 2.1	8
			Coll	-37.7 ± 1.7	3.3 ± 1.0	3	-34.0 ± 1.5	2.8 ± 0.2	3	-35.0 ± 3.5	2.9 ± 1.0	3
			Graz	-	-	-	-	-	-	-	-	-
			Shred	-	-	-	-33.4 ± 0.4	2.1 ± 0.8	3	-32.6 ± 0.3	1.0 ± 0.2	2
			T-INV	-27.6 ± 1.7	4.5 ± 3.3	3	-27.8 ± 2.8	2.8 ± 1.9	3	-28.6	7.7	1
			CARC	-	-	-	-	-	-	-	-	-
			EGG	-	-	-	-	-	-	-	-	-
			CHIN	-	-	-	-29.1	8.2	1	-	-	-
			COHO	-	-	-	-28.5 ± 2.1	7.3 ± 1.2	14	-28.0 ± 2.5	8.3 ± 1.0	6
		TM	PERI	-33.0 ± 0.5	2.9 ± 0.2	3	-30.9 ± 0.0	1.8 ± 0.1	3	-31.1 ± 1.2	6.4 ± 3.0	3
			OMS	-27.3 ± 0.8	-0.1 ± 0.3	2	-27.8 ± 0.4	-0.5 ± 0.0	2	-27.5 ± 0.3	0.2 ± 0.6	2
			OMB	-27.8 ± 0.5	0.6 ± 1.2	3	-28.0 ± 0.3	-1.6 ± 0.8	3	-28.5 ± 1.1	-1.5 ± 0.7	3
			A-INV	-32.7 ± 2.4	5.0 ± 1.2	9	-33.0 ± 1.1	4.6 ± 1.1	6	-32.0 ± 2.3	4.8 ± 1.1	8
			Coll	-31.9 ± 2.6	4.5 ± 0.4	3	-32.9 ± 1.5	4.3 ± 0.5	3	-31.8 ± 2.0	4.8 ± 0.9	3
			Graz	-31.5 ± 0.1	4.5 ± 0.2	3	-	-	-	-34.2 ± 3.1	5.1 ± 0.6	2
			Shred	-35.0 ± 3.4	5.0 ± 2.1	3	-32.9	3.0	1	-30.6 ± 3.2	3.4 ± 0.9	3

		T-INV	-27.6	3.9	1	-	-	-	-26.2	2.3	1
		CARC	-	-	-	-	-	-	-19.2	11.9	1
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-27.4 ± 1.2	8.3 ± 0.3	8	-	-	-	-	-	-
		COHO	-	-	-	-27.4 ± 1.5	8.9 ± 0.8	16	-25.1 ± 2.3	9.6 ± 1.7	14
	SC	PERI	-23.9 ± 0.2	3.2 ± 0.1	3	-23.5 ± 3.6	1.4 ± 1.7	3	-27.5 ± 4.1	0.1 ± 2.0	3
		OMS	-27.0 ± 0.1	-0.3 ± 0.4	2	-27.1 ± 0.0	-4.0 ± 0.1	2	-28.6 ± 1.7	-0.4 ± 0.6	2
		OMB	-28.0 ± 0.2	-0.7 ± 0.3	3	-26.2 ± 0.9	-4.4 ± 0.7	3	-29.9 ± 0.8	-1.2 ± 0.8	3
		A-INV	-31.0 ± 1.7	4.1 ± 1.6	5	-26.2 ± 0.7	3.5 ± 0.9	9	-26.0 ± 2.8	1.2 ± 3.3	8
		Coll	-29.7	3.1	1	-25.9 ± 1.1	3.4 ± 1.3	3	-26.2 ± 2.6	3.6 ± 4.5	3
		Graz	-	-	-	-26.3 ± 0.3	3.8 ± 1.1	3	-27.3 ± 0.1	3.4 ± 0.2	2
		Shred	-29.6	2.2	1	-	-	-	-26.5 ± 0.9	0.3 ± 0.7	3
		T-INV	-28.3 ± 2.6	3.0 ± 2.4	3	-25.4 ± 1.0	3.3 ± 1.9	2	-25.2 ± 1.1	1.5 ± 2.8	3
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-	-	-	-	-	-	-	-	-
		COHO	-	-	-	-26.3 ± 2.8	8.6 ± 1.1	15	-24.4 ± 3.2	9.6 ± 1.9	12
	3	TM	PERI	-26.6 ± 2.9	4.5 ± 1.0	3	-27.6 ± 1.0	4.7 ± 0.0	2	-30.5 ± 1.0	1.5 ± 1.9	3
			OMS	-27.3 ± 0.4	-0.3 ± 0.2	2	-29.1 ± 0.0	0.8 ± 0.6	2	-28.2 ± 0.4	0.6 ± 0.1	2
			OMB	-27.3 ± 1.1	-1.0 ± 0.4	3	-27.8 ± 0.5	-0.0 ± 0.5	3	-27.8 ± 0.3	2.6 ± 0.6	3
			A-INV	-29.3 ± 2.8	2.9 ± 1.8	9	-28.0 ± 1.5	4.3 ± 1.1	9	-27.3 ± 1.3	4.1 ± 1.1	9
			Coll	-31.6 ± 0.8	2.5 ± 0.5	3	-26.7 ± 1.7	4.6 ± 0.9	3	-27.2 ± 0.7	3.4 ± 0.9	3
			Graz	-30.0 ± 2.7	3.0 ± 0.1	3	-29.4 ± 1.0	5.0 ± 0.3	3	-28.6 ± 2.0	4.5 ± 0.7	3
			Shred	-28.9 ± 3.9	1.8 ± 2.3	3	-27.6 ± 1.9	2.8 ± 0.8	3	-26.4 ± 0.2	3.0 ± 0.7	3
			T-INV	-26.1 ± 1.8	1.9 ± 1.8	2	-28.0	5.2	1	-25.6 ± 1.6	1.7 ± 2.0	2
			CARC	-	-	-	-19.5 ± 0.5	10. ± 0.6	7	-19.4 ± 0.0	11.2 ± 0.5	3
			EGG	-	-	-	-23.4 ± 0.8	11.3 ± 0.0	2	-	-	-
			CHIN	-24.7 ± 0.9	9.7 ± 0.6	3	-22.9 ± 1.0	9.4 ± 1.4	3	-23.6 ± 1.8	9.7 ± 1.3	5
			COHO	-26.7 ± 1.7	8.4 ± 1.1	13	-23.1 ± 1.7	9.2 ± 1.7	10	-23.3 ± 1.5	9.1 ± 1.5	9
2014	1	US	PERI	-31.9 ± 0.5	1.1 ± 1.0	3	-32.8 ± 0.4	1.3 ± 0.1	3	-31.5 ± 0.6	1.7 ± 0.9	3
			OMS	-29.0 ± 0.8	3.0 ± 1.2	2	-27.9 ± 0.5	-0.3 ± 2.1	2	-28.3 ± 0.7	2.9 ± 0.5	2
			OMB	-30.3 ± 1.1	0.2 ± 1.5	3	-28.1 ± 0.3	1.3 ± 0.1	3	-28.7 ± 1.0	0.0 ± 1.2	3
			A-INV	-33.0 ± 4.3	2.7 ± 1.2	6	-33.7 ± 4.5	3.9 ± 3.1	9	-32.0 ± 3.5	4.6 ± 1.1	5
			Coll	-35.7 ± 1.7	3.4 ± 0.3	3	-38.1 ± 1.4	4.5 ± 0.9	5	-33.4 ± 3.6	4.3 ± 1.1	4
			Graz	-33.4	2.1	1	-	-	-	-	-	-
			Shred	-26.3 ± 0.1	1.0 ± 0.6	2	-30.8 ± 3.9	0.8 ± 4.1	4	-29.2	4.4	1
			T-INV	-29.5	6.8	1	-25.8 ± 0.8	2.3 ± 3.8	3	-27.8 ± 1.0	2.7 ± 4.2	3
			CARC	-	-	-	-19.9	12.6	1	-	-	-
			EGG	-	-	-	-	-	-	-	-	-
			CHIN	-32.7	6.7	1	-25.2 ± 0.7	8.4 ± 0.7	4	-	-	-
			COHO	-27.4 ± 2.3	9.7 ± 1.5	8	-27.2 ± 1.9	8.0 ± 0.5	8	-26.4 ± 1.6	9.3 ± 1.5	13
		TM	PERI	-30.0 ± 0.2	2.0 ± 0.4	3	-28.1 ± 1.2	4.4 ± 1.3	3	-23.4 ± 0.6	2.4 ± 1.3	3
			OMS	-28.4 ± 0.1	-1.4 ± 0.6	2	-28.1 ± 0.1	1.8 ± 0.1	2	-28.7 ± 0.3	-0.8 ± 0.1	2
			OMB	-27.7 ± 1.5	-1.5 ± 0.9	3	-28.2 ± 0.8	0.2 ± 0.5	3	-27.7 ± 0.2	-0.2 ± 0.3	3
			A-INV	-27.2 ± 1.2	4.3 ± 1.7	9	-28.2 ± 1.7	5.0 ± 1.0	14	-26.7 ± 1.0	4.8 ± 1.0	11
			Coll	-27.8 ± 0.1	4.0 ± 0.6	3	-28.3 ± 1.6	4.9 ± 0.5	5	-26.5 ± 1.5	4.6 ± 1.2	5
			Graz	-28.6 ± 0.1	2.8 ± 0.6	2	-29.8 ± 0.5	4.3 ± 0.4	5	-26.0	4.5	1
			Shred	-26.8	2.1	1	-26.9 ± 1.2	5.0 ± 0.6	4	-27.2 ± 0.8	4.6 ± 1.1	5
			T-INV	-26.9 ± 0.3	3.3 ± 0.6	3	-26.1	4.0	1	-24.6 ± 1.1	5.8 ± 2.5	2
			CARC	-	-	-	-20.4 ± 0.1	11.6 ± 0.9	2	-	-	-
			EGG	-	-	-				-	-	-
			CHIN	-	-	-	-25.6 ± 0.2	8.2 ± 0.3	7	-	-	-
			COHO	-25.5 ± 1.7	10.0 ± 2.2	6	-26.3 ± 1.0	8.5 ± 0.4	7	-28.4 ± 1.2	7.2 ± 0.5	2

	SC	PERI	-25.4 ± 0.5	2.2 ± 0.4	3	-24.5 ± 1.4	2.0 ± 0.9	2	-23.1 ± 0.7	4.9 ± 0.6	3
		OMS	-27.7 ± 0.1	-1.3 ± 0.4	2	-27.1 ± 0.1	-0.5 ± 0.1	2	-27.5 ± 0.1	-0.6 ± 0.1	2
		OMB	-27.6 ± 0.3	-2.2 ± 0.3	3	-27.2 ± 0.1	-1.2 ± 0.1	3	-27.5 ± 0.6	-1.5 ± 0.4	3
		A-INV	-26.9 ± 1.6	1.5 ± 1.4	11	-26.2 ± 0.4	2.3 ± 1.3	6	-24.9 ± 2.3	3.8 ± 0.5	5
		Coll	-27.0 ± 1.7	1.9 ± 1.0	5	-26.3 ± 0.5	1.8 ± 1.0	5	-26.1 ± 3.2	3.6 ± 0.6	4
		Graz	-25.6 ± 0.5	0.6 ± 1.4	4	-26.3	5.2	1	-24.9	3.2	1
		Shred	-25.8 ± 1.0	-0.2 ± 0.8	2	-	-	-	-	-	-
		T-INV	-26.5 ± 0.6	-0.8 ± 0.6	2	-26.1	1.2	1	-	-	-
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-26.6 ± 1.1	8.3 ± 0.6	5	-25.5 ± 0.5	6.5 ± 0.4	3	-25.6 ± 1.1	6.3 ± 0.6	6
		COHO	-31.2	6.7	1	-	-	-	-	-	-
	MC	PERI	-25.1 ± 0.1	0.0 ± 0.3	3	-22.6 ± 1	-0.3 ± 0.3	3	-21.5 ± 0.2	1.5 ± 1.7	3
		OMS	-28.2 ± 0..1	-2.8 ± 0.6	2	-27.1 ± 0.1	-0.5 ± 0.1	2	-28.4 ± 0.8	-0.6 ± 0.1	2
		OMB	-27.5 ± 0.1	-1.4 ± 0.2	3	-27.2 ± 0.1	-1.2 ± 0.1	3	-28 ± 0.6	-1.6 ± 0.3	3
		A-INV	-27.5 ± 1.2	2.5 ± 1.3	11	-26.2 ± 0.9	1.7 ± 1.3	8	-25.1 ± 1.5	2.7 ± 0.8	7
		Coll	-27.3 ± 0.5	1.9 ± 0.9	5	-25.5 ± 0.8	1.5 ± 0.7	5	-24.3 ± 1.4	2.7 ± 1.2	3
		Graz	-26.4 ± 0.3	2.5 ± 0.6	3	-26.3 ± 0.3	-0.4 ± 0.1	2	-24.4	2.1	1
		Shred	-27.5 ± 1.0	1.5 ± 1.8	3	-27.6	1.5	1	-26.2 ± 1.2	2.6 ± 0.9	3
		T-INV	-25.1 ± 1.2	3.6 ± 3.3	2	-24.2 ± 2.0	-1.7 ± 0.8	2	-25.9 ± 0.1	-0.4 ± 1.2	2
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-26.8 ± 0.3	7.6 ± 1.5	3	-25.3 ± 0.4	5.5 ± 0.5	8	-24.6 ± 0.6	7.9 ± 1.7	6
		COHO	-26.6 ± 1.9	8.7 ± 2.3	7	-	-	-	-	-	-
2	US	PERI	-31.7 ± 1.9	0.8 ± 0.5	3	-33.5 ± 2.9	1.9 ± 0.6	3	-33.3 ± 2.0	2.1 ± 0.2	3
		OMS	-30.1 ± 2.9	-1.0 ± 0.7	2	-34.6 ± 0.1	1.7 ± 0.5	2	-28.5 ± 0.1	0.5 ± 0.1	2
		OMB	-27.7 ± 0.3	-2.3 ± 0.1	3	-27.4 ± 0.8	-0.3 ± 0.3	3	-28.3 ± 0.8	-1.1 ± 0.6	3
		A-INV	-33.0 ± 3.1	2.6 ± 1.0	8	-36.4 ± 3	2.6 ± 1.2	9	-35.8 ± 3.7	3.0 ± 1.9	15
		Coll	-34.5 ± 1.8	2.1 ± 0.5	5	-37.7 ± 3	2.1 ± 1.1	5	-36.2 ± 2.6	2.6 ± 0.7	5
		Graz	-	-	-	-	-	-	-	-	-
		Shred	-34.7 ± 2.9	2.6 ± 1.2	3	-35.8 ± 0.8	2.3 ± 1.1	4	-36.1 ± 2.5	2.9 ± 0.9	5
		T-INV	-25.5 ± 0.7	-0.7 ± 0.7	2	-26.7 ± 1	3.6 ± 0.3	3	-26.7 ± 1.2	2.2 ± 0.4	2
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-	-	-	-32.3 ± 0.4	5.4 ± 0.2	6	-34.0	6.3	1
		COHO	-29.2 ± 1.1	8.4 ± 1.4	8	-31.3 ± 1.9	6.2 ± 0.8	7	-31.1 ± 1.5	7.1 ± 0.8	8
	SS	PERI	-32.6 ± 1.7	2.3 ± 0.3	3	-28.2 ± 2.8	2.1 ± 1.7	3	-33.8 ± 1.1	2.1 ± 2.0	3
		OMS	-28.0 ± 0.1	-1.8 ± 0.1	2	-26.9 ± 0.1	-0.4 ± 0.6	2	-27.9 ± 0.6	1.1 ± 0.5	2
		OMB	-28.6 ± 0.6	-1.2 ± 1.1	3	-28.1 ± 0.8	-0.4 ± 0.3	3	-29.1 ± 0.8	-0.4 ± 1.1	3
		A-INV	-33.3 ± 2.9	3.1 ± 1.9	14	-33.5 ± 2.9	2.8 ± 1.0	10	-35.3 ± 3.5	3.4 ± 0.8	7
		Coll	-35.0 ± 1.4	2.3 ± 0.9	5	-35.1 ± 1.2	2.0 ± 0.8	5	-37.2 ± 1.9	3.4 ± 0.6	5
		Graz	-39.7	3.2	1	-38.1	2.6	1	-30.4 ± 4.0	4.1 ± 1.4	2
		Shred	-32.0 ± 2.3	3.3 ± 2.3	8	-31.7 ± 2.3	3.2 ± 0.6	4	-	-	-
		T-INV	-27.1 ± 1.6	1.1 ± 2.7	2	-27.3 ± 0.8	4.5 ± 1.3	2	-26.3	4.8	1
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-	-	-	-27.2 ± 0.6	6.2 ± 0.4	3	-	-	-
		COHO	-29.1 ± 0.7	7.8 ± 1.0	6	-26.7 ± 0.8	7.6 ± 0.5	5	-27.8 ± 2.5	8.7 ± 1.2	10
	TM	PERI	-30.1 ± 0.2	3.3 ± 0.4	3	-30.6 ± 0.6	2.5 ± 0.6	3	-28.4 ± 0.2	3.6 ± 1.4	3
		OMS	-28.4 ± 0.2	1.2 ± 0.5	2	-27.8 ± 0.1	2.0 ± 1.0	2	-28.6 ± 0.7	-0.1 ± 0.1	2
		OMB	-28.3 ± 0.3	-1.0 ± 0.1	3	-27.8 ± 0.6	0.5 ± 1.6	3	-29.0 ± 0.4	1.6 ± 1.1	3
		A-INV	-32.2 ± 0.9	4.8 ± 0.9	5	-31.8 ± 0.9	4.3 ± 0.9	11	-30.7 ± 1.5	4.7 ± 1.3	8

		Coll	-32.5 ± 1.1	4.3 ± 0.7	5	-32.0 ± 0.7	4.3 ± 0.3	5	-30.1 ± 1.9	4.9 ± 1.4	3
		Graz	-	-	-	-34.1	3.9	1	-	-	-
		Shred	-	-	-	-31.6 ± 0.6	3.6 ± 1.0	5	-30.9 ± 1.6	3.9 ± 1.5	5
		T-INV	-	-	-	-25.1	6.9	1	-	-	-
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-27.9 ± 1.0	8.4 ± 0.6	6	-27.6 ± 0.1	7.0 ± 0.8	2	-27.8 ± 1.2	8.2 ± 1.0	8
		COHO	-28.1 ± 1.4	8.1 ± 0.9	10	-27.8 ± 0.5	7.3 ± 0.4	6	-27.4 ± 0.8	8.2 ± 0.6	8
	SC	PERI	-24.9 ± 0.5	0.1 ± 0.6	3	-21.8 ± 0.9	1.2 ± 1.7	3	-23.1 ± 2.4	0.3 ± 1.0	3
		OMS	-27.0 ± 0.1	-2.1 ± 0.3	2	-26.5 ± 0	0.0 ± 0.2	2	-27.1 ± 1.1	0.2 ± 0.4	2
		OMB	-27.8 ± 0.4	-1.5 ± 0.6	3	-25.9 ± 0.4	0.0 ± 0.4	3	-28.0 ± 0.7	-0.7 ± 0.4	3
		A-INV	-28.7 ± 3.2	2.3 ± 0.7	8	-25.8 ± 1.6	1.4 ± 0.8	8	-23.4 ± 0.9	1.6 ± 1.5	7
		Coll	-29.2 ± 4.3	2.4 ± 0.9	5	-24.3 ± 1.1	0.7 ± 0.5	5	-23.5 ± 1.2	0.7 ± 1.7	5
		Graz	-28.8 ± 0.5	2.5 ± 0.3	3	-26.9 ± 0.9	2.2 ± 0.1	3	-	-	-
		Shred	-	-	-	-	-	-	-24.3 ± 0.5	2.7 ± 2.1	2
		T-INV	-24.1 ± 0.3	0.7 ± 0.1	2	-22.8	0.4	1	-	-	-
		CARC	-	-	-	-	-	-	-20.8	10.6	1
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-	-	-	-25.2 ± 0.2	5.5 ± 0.4	7	-25.8 ± 2.2	6.5 ± 0.7	7
		COHO	-27.6 ± 0.3	7.6 ± 0.2	2	-27.5 ± 2.6	7.9 ± 1.5	5	-26.0 ± 0.3	6.7 ± 1.0	5
	MC	PERI	-25.5 ± 0.3	-0.3 ± 0.3	3	-23.3 ± 1.8	1.5 ± 0.7	3	-24.2 ± 2.0	-0.3 ± 3.0	3
		OMS	-27.2 ± 0.2	-1.1 ± 1.0	2	-26.5 ± 0.1	-0.4 ± 0.1	2	-27.4 ± 0.1	-0.7 ± 0.5	2
		OMB	-28.1 ± 0.2	-2.2 ± 0.9	3	-26.8 ± 0.6	-0.9 ± 0.1	3	-28.1 ± 1.0	-1.1 ± 0.3	3
		A-INV	-27.9 ± 1.4	4.0 ± 1.5	7	-27.9 ± 0.9	2 ± 0.9	5	-24.4 ± 1.8	2.0 ± 1.0	7
		Coll	-27.6 ± 1.5	3.4 ± 1.7	5	-28.4 ± 0.9	1.3 ± 0.6	3	-23.7 ± 0.8	1.1 ± 0.6	5
		Graz	-	-	-	-27.2 ± 1.3	3.2 ± 1.3	2	-24.9	4.2	1
		Shred	-26.7 ± 1.1	5.5 ± 1.4	2	-	-	-	-29.4	2.5	1
		T-INV	-24.4	-0.3	1	-24.1	1.4	1	-	-	-
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-26.8 ± 0.7	7.7 ± 0.7	2	-25.3 ± 0.3	6.2 ± 0.4	10	-24.2 ± 1.0	7.0 ± 0.2	4
		COHO	-	-	-	-	-	-	-	-	-
3	US	PERI	-28.0 ± 2.5	0.0 ± 0.3	3	-29.1 ± 2.1	0.9 ± 1.8	3	-26.7 ± 2.8	0.0 ± 0.2	3
		OMS	-28.8 ± 2.1	-2.5 ± 0.3	2	-27.0 ± 0.4	-0.8 ± 0.9	2	-27.9 ± 0	0.8 ± 0.1	2
		OMB	-28.1 ± 0.5	-1.4 ± 0.3	3	-27.7 ± 0.9	-0.5 ± 0.5	3	-28.8 ± 0.8	-0.9 ± 0.9	3
		A-INV	-28.2 ± 1.1	2.6 ± 1.8	9	-29.9 ± 0.7	0.7 ± 3.0	10	-27.9 ± 1.4	3.1 ± 1.4	6
		Coll	-28.4 ± 0.5	2.8 ± 0.5	5	-29.7 ± 0.6	2.1 ± 0.8	5	-26.6 ± 0.6	4.5 ± 0.4	3
		Graz	-30.0	-1.1	1	-30.0 ± 0.1	2.2 ± 0.1	1	-	-	-
		Shred	-27.1 ± 1.2	1.7 ± 1.0	3	-30.2 ± 0.9	-1.3 ± 4.2	4	-28.9 ± 1	2.2 ± 1.4	3
		T-INV	-26.5 ± 1.1	2.4 ± 3.0	3	-28.9 ± 3.3	2.2 ± 2.8	2	-25.8	2.1	1
		CARC	-	-	-	-	-	-	-20.3 ± 0.6	11.4 ± 0.4	4
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-27.9	6.0	1	-25.6 ± 0.3	6.4 ± 1.3	5	-25.5 ± 0.6	7.7 ± 0.8	3
		COHO	-	-	-	-	-	-	-	-	-
	TM	PERI	-28.2 ± 0.6	0.9 ± 0.1	3	-31.0 ± 1.3	2.5 ± 0.1	2	-28.5 ± 0.4	1.2 ± 0.6	3
		OMS	-29.2 ± 0.3	-1.3 ± 0.3	2	-28.3 ± 0.2	0.6 ± 0.2	2	-28.8 ± 0.2	-0.1 ± 0.2	2
		OMB	-28.6 ± 0.4	-1.5 ± 0.5	3	-27.6 ± 0.3	-0.5 ± 0.7	3	-28.5 ± 0.7	-0.3 ± 0.2	3
		A-INV	-28.0 ± 1.4	3.2 ± 2.0	15	-28.8 ± 1.2	2.5 ± 0.8	17	-28.8 ± 1.2	3.0 ± 0.8	14
		Coll	-28.7 ± 1.2	2.1 ± 1.7	5	-28.4 ± 0.5	2.2 ± 0.4	6	-28.5 ± 1.3	2.5 ± 0.4	5
		Graz	-29.2 ± 1.3	1.8 ± 0.3	5	-30.4 ± 0.5	2.8 ± 0.4	5	-29.8 ± 0.3	3.6 ± 0.5	5
		Shred	-26.9 ± 0.4	4.2 ± 1.7	5	-27.4 ± 0.5	1.0 ± 0.7	2	-27.4 ± 0.4	2.4 ± 0.5	4
		T-INV	-25.4 ± 0.7	1.4 ± 0.3	2	-27.0 ± 0.6	0.3 ± 1.5	2	-26.4 ± 1.1	2.3 ± 0.1	2
		CARC	-	-	-	-18.2	13.7	1	-	-	-

		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-26.3	8.6	1	-26.3 ± 0.5	6.1 ± 0.3	8	-25.0 ± 1.0	9.4 ± 1.1	7
		COHO	-26.1 ± 0.9	8.6 ± 0.9	7	-	-	-	-	-	-
	SC	PERI	-21.2 ± 0.9	0.1 ± 1.0	3	-24.3 ± 0.6	0.6 ± 0.1	3	-21.5 ± 1.2	1.7 ± 4.4	3
		OMS	-27.3 ± 0.5	-1.5 ± 0.2	2	-26.5 ± 0.1	0.0 ± 0.1	2	-24.5 ± 0.6	-0.3 ± 0.5	2
		OMB	-26.6 ± 0.1	-0.2 ± 0.2	3	-26.9 ± 0.5	0.0 ± 0.3	3	-27.2 ± 1.1	-0.6 ± 0.4	3
		A-INV	-28.9 ± 1.7	2.1 ± 1.2	6	-28.5 ± 1.2	1.4 ± 1.2	9	-21.9 ± 1.2	1.7 ± 0.5	3
		Coll	-27.8 ± 1.1	1.5 ± 1.0	5	-27.5 ± 1.0	0.6 ± 0.3	5	-20.9 ± 0.7	1.2 ± 0.2	3
		Graz	-29.7	3.5	1	-30.0 ± 0.8	1.1 ± 0.6	3	-	-	-
		Shred	-	-	-	-28.4	-0.2	1	-	-	-
		T-INV	-29.2 ± 2.9	2.8 ± 2.4	2	-26.2 ± 0.4	2.6 ± 0.1	2	-25.1	3.6	1
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-27.7 ± 0.3	6.6 ± 0.5	4	-25.7 ± 0.2	6.0 ± 0.4	8	-24.7 ± 0.6	6.2 ± 0.3	8
		COHO	-26.1	9.6	1	-	-	-	-	-	-
	MC	PERI	-25.6 ± 0.1	1.7 ± 0.1	3	-26.9 ± 1.4	0.4 ± 0.1	3	-27.7 ± 0.2	1.8 ± 0.6	3
		OMS	-27.5 ± 0.1	-1.4 ± 0.1	2	-26.6 ± 0.4	-0.3 ± 0.1	2	-27.5 ± 0.1	-1.1 ± 0.2	2
		OMB	-27.6 ± 0.2	-1.8 ± 1.0	3	-27.0 ± 0.2	-1.1 ± 0.2	3	-28.3 ± 1.2	-1.4 ± 0.2	3
		A-INV	-28.7 ± 3.2	2.5 ± 1.3	6	-28.4 ± 1.2	1.8 ± 1.1	8	-25.0 ± 1.4	2.1 ± 0.8	10
		Coll	-28.8 ± 4.0	2.2 ± 1.5	5	-28.6 ± 1.7	1.1 ± 0.7	5	-23.6 ± 0.7	1.8 ± 0.3	5
		Graz	-26.4	2.0	1	-27.7 ± 1.1	1.4 ± 0.8	3	-25.7 ± 1.9	2.7 ± 0.3	3
		Shred	-	-	-	-	-	-	-26.2 ± 0.5	0.4 ± 0.1	2
		T-INV	-28.2 ± 4.8	2.1 ± 1.4	2	-26.8	-0.7	1	-25.0	5.0	1
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-27.0 ± 0.7	6.9 ± 0.8	8	-25.8 ± 0.3	6.7 ± 0.3	8	-24.9 ± 0.5	7.0 ± 0.8	8
		COHO	-	-	-	-	-	-	-	-	-
4	SC	PERI	-25.2 ± 0.7	3.3 ± 0.4	3	-20.5 ± 0.9	-0.3 ± 1.2	3	-25.8 ± 2.8	0.1 ± 0.4	3
		OMS	-27.1 ± 0.1	-1.3 ± 0.3	2	-26.2 ± 0.4	1.5 ± 3.1	2	-27.1 ± 0.1	-0.9 ± 0.1	2
		OMB	-26.9 ± 0.2	-2.7 ± 0.5	3	-26.5 ± 0.4	-0.6 ± 0.3	3	-27.8 ± 0.8	-1.1 ± 0.4	3
		A-INV	-29.0 ± 1.9	2.8 ± 1.0	7	-27.4 ± 1.5	2.1 ± 0.8	7	-26.3 ± 1.1	3 ± 0.4	12
		Coll	-27.9 ± 1.4	2.4 ± 0.2	5	-26.2 ± 1.8	1.7 ± 0.3	4	-26.2 ± 1.4	2.8 ± 0.1	5
		Graz	-	-	-	-27.7 ± 0.8	2.7 ± 0.9	3	-	-	-
		Shred	-29.1 ± 2.9	3.6 ± 1.4	2	-	-	-	-26.9 ± 1	2.6 ± 0.5	2
		T-INV				-25.0 ± 0.1	0.2 ± 1.2	2	-	-	-
		CARC	-	-	-	-	-	-	-	-	-
		EGG	-	-	-	-	-	-	-	-	-
		CHIN	-26.6 ± 0.4	6.9 ± 0.4	3	-	-	-	-	-	-
		COHO	-	-	-	-	-	-	-	-	-

A-2. Percent mean weight (%MW) of freshwater, marine, and terrestrial prey categories found in the stomachs of juvenile Chinook (CK) and (or) Coho (CO) salmon captured in study sites. Values pooled by season are shown in bold. Values in the "Reach" category are represented as distance (river kilometers) from the mouth of the Susitna River. Note: sampling events where $n \leq 2$ were not included in the stomach content analysis.

Year	Season	Reach	Macrohabitat type	Consumer species (n)	%MW ± SD		
					Freshwater	Marine	Terrestrial
2013	Spring	**All**	**All**	**CK, CO (41)**	**78.4 ± 27.1**	**0.0**	**21.7 ± 27.1**
		1	Upland slough	CK (7), CO (6)	71.1 ± 24.9	0.0	28.9 ± 24.9
			Tributary mouth	CK (8), CO (7)	70.7 ± 28.9	0.0	29.3 ± 28.9
		2	Tributary mouth	CK (4)	97.2 ± 5.5	0.0	2.8 ± 5.5
		3	Tributary mouth	CK (2), CO (7)	88.7 ± 29.0	0.0	11.3 ± 29.0
	Summer	**All**	**All**	**CK, CO (64)**	**55.6 ± 44.0**	**27.1 ± 43.8**	**17.2 ± 30.1**
		1	Tributary mouth	CK (1), CO (4)	62.2 ± 46.1	19.4 ± 43.4	18.4 ± 31.8
		2	Tributary mouth	CK (2), CO (21)	64.1 ± 38.9	16.5 ± 36.9	19.4 ± 28.2
			Upland slough	CK (1), CO (13)	93.6 ± 5.1	0.0	6.4 ± 12.3
			Side channel	CO (9)	41.5 ± 47.9	11.1 ± 33.3	47.4 ± 48.6
		3	Tributary mouth	CK (3), CO (10)	7.0 ± 13.5	89.1 ± 27.1	3.9 ± 13.9
	Fall	**All**	**All**	**CK, CO (56)**	**27.7 ± 39.0**	**53.7 ± 47.4**	**18.6 ± 33.0**
		1	Upland slough	CO (3)	34.4 ± 56.9	0.0	65.6 ± 56.9
		2	Tributary mouth	CO (23)	19.0 ± 32.5	67.9 ± 45.1	13.1 ± 33.4
			Upland slough	CO (5)	84.3 ± 32.1	12.8 ± 28.6	2.9 ± 4.2
			Side channel	CO (11)	27.4 ± 28.9	32.9 ± 45.9	39.7 ± 33.7
		3	Tributary mouth	CK (5), CO (7)	26.5 ± 44.4	72.0 ± 44.0	1.4 ± 5.1
2014	Spring	**All**	**All**	**CK, CO (72)**	**81.1 ± 29.7**	**0.0**	**18.8 ± 29.7**
		1	Upland slough	CO (6)	63.9 ± 49.9	0.0	36.1 ± 49.9
			Tributary mouth	CO (4)	90.7 ± 18.2	0.0	9.3 ± 18.2
			Side channel	CK (5), CO (1)	88.4 ± 15.1	0.0	11.6 ± 15.1
			Main channel	CK (3), CO (6)	83.5 ± 28.7	0.0	16.5 ± 28.7
		2	Upland slough	CO (4)	95.5 ± 9.0	0.0	4.5 ± 9.0
			Side slough	CO (5)	79.9 ± 27.7	0.0	20.1 ± 27.6
			Tributary mouth	CK (6), CO (10)	74.4 ± 38.8	0.0	25.6 ± 38.8
		3	Tributary mouth	CK (1), CO (5)	72.2 ± 30.5	0.0	27.8 ± 30.5
			Side channel	CK (4), CO (1)	73.7 ± 36.4	0.0	26.3 ± 36.4
			Main channel	CK (8)	90.3 ± 9.7	0.0	9.7 ± 9.7
		4	Side channel	CK (3)	94.7 ± 4.8	0.0	5.3 ± 4.8
	Summer	**All**	**All**	**CK, CO (111)**	**79.2 ± 29.1**	**0.7 ± 7.3**	**20.1 ± 28.4**
		1	Upland slough	CK (4), CO (8)	87.5 ± 23.8	0.0	12.5 ± 23.8
			Tributary mouth	CK (6), CO (6)	86.7 ± 24.9	0.0	13.2 ± 24.9
			Side channel	CK (3)	67.9 ± 18.9	0.0	32.1 ± 19.2
			Main channel	CK (8)	66.8 ± 22.9	0.0	33.2 ± 22.9
		2	Upland slough	CK (6), CO (7)	91.4 ± 17.7	0.0	8.6 ± 17.7
			Side slough	CK (2), CO (2)	46.9 ± 51.9	0.0	53.1 ± 51.9
			Tributary mouth	CK (2), CO (6)	84.2 ± 24.6	0.0	15.8 ± 24.6

		Side channel	CK (7), CO (5)	64.7 ± 42.2	0.0	35.3 ± 42.2
		Main channel	CK (10)	83.3 ± 16.8	0.0	16.7 ± 16.8
	3	Upland slough	CK (5)	98.7 ± 2.5	0.0	1.3 ± 2.5
		Tributary mouth	CK (7)	88.2 ± 30.6	9.7 ± 27.3	2.1 ± 3.9
		Side channel	CK (8)	83.2 ± 26.4	0.0	16.8 ± 26.4
		Main channel	CK (8)	55.4 ± 31.1	0.0	44.6 ± 31.1
Fall	**All**	**All**	**CK, CO (94)**	**73.4 ± 36.5**	**3.7 ± 17.1**	**22.9 ± 33.8**
	1	Upland slough	CO (12)	57.2 ± 39.6	12.7 ± 30.6	30.2 ± 32.5
		Side channel	CK (3)	33.3 ± 57.7	0.0	66.7 ± 57.7
		Main channel	CK (6)	94.3 ± 8.0	0.0	5.7 ± 8.0
	2	Upland slough	CK (1), CO (8)	96.4 ± 16.5	0.0	3.6 ± 6.5
		Side slough	CO (8)	52.7 ± 45.3	36.7 ± 50.6	10.7 ± 19.7
		Tributary mouth	CK (8), CO (8)	86.0 ±26.8	5.8 ± 23.3	8.2 ± 16.5
		Side channel	CK (7), CO (5)	68.2 ± 36.8	0.0	31.8 ± 36.8
		Main channel	CK (4)	97.1 ± 5.9	0.0	2.9 ± 5.9
	3	Upland slough	CK (3)	28.4 ± 30.9	58.1 ± 50.5	13.4 ± 20.1
		Tributary mouth	CK (7)	100.0	0.0	0.0
		Side channel	CK (8)	99.9 ± 0.3	0.0	0.1 ± 0.3
		Main channel	CK (8)	98.3 ± 3.1	0.0	1.7 ± 3.1

A-3. Results of MixSIAR Bayesian stable isotope diet models performed for juvenile Chinook and Coho salmon consumers (pooled) and the potential freshwater, marine, and terrestrial prey categories for all study sites in 2013 and 2014. Values in the "Reach" category are represented as distance (river kilometers) from the mouth of the Susitna River.

Year	Season	Reach	Macrohabitat type	Consumer species (n)	Mean % contribution (2.5%, 97.5% CI)		
					Freshwater	Marine	Terrestrial
2013	Spring	1	Upland slough	CK (6), CO (8)	58.3 (35.6, 80.5)	3.0 (0.1, 11.0)	38.7 (16.7, 61.1)
			Tributary mouth	CK (7), CO (10)	57.3 (38.0, 77.7)	9.9 (0.7, 23.1)	32.9 (14.3, 54.4)
		2	Tributary mouth	CK (8)	51.5 (25.2, 82.0)	11.8 (1.2, 25.5)	36.7 (7.6, 65.0)
		3	Tributary mouth	CK (3), CO (13)	60.9 (43.1, 76.2)	23.6 (10.9, 34.3)	15.4 (2.7, 34.9)
	Summer	1	Tributary mouth	CK (1), CO (3)	48.3 (15.3, 81.0)	22.0 (2.2, 56.2)	29.7 (5.0, 64.3)
		2	Tributary mouth	CK (1), CO (15)	69.0 (51.7, 84.9)	16.1 (4.8, 26.2)	14.9 (1.8, 33.8)
			Upland slough	CK (1), CO (14)	50.9 (38.8, 63.7)	23.1 (16.1, 29.7)	26.0 (14.8, 38.5)
			Side channel	CO (15)	41.0 (18.2, 65.9)	15.7 (3.5, 29.9)	43.3 (20.1, 69.1)
		3	Tributary mouth	CK (3), CO (10)	31.9 (14.7, 54.0)	47.3 (34.0, 63.7)	20.7 (3.4, 39.0)
	Fall	1	Upland slough	CO (5)	37.6 (7.4, 74.5)	27.3 (2.1, 56.6)	35.1 (7.0, 71.2)
		2	Tributary mouth	CO (14)	63.0 (34.4, 91.1)	18.9 (1.3, 39.0)	18.1 (0.8, 48.8)
			Upland slough	CO (6)	31.0 (17.6, 45.2)	40.3 (33.7, 53.4)	26.0 (14.5, 38.5)
			Side channel	CO (12)	27.7 (9.3, 51.5)	35.0 (15.5, 54.7)	37.3 (15.5, 62.0)
		3	Tributary mouth	CK (5), CO (9)	40.5 (20.1, 60.0)	43.6 (31.8, 57.4)	15.9 (1.9, 35.1)
2014	Spring	1	Upland slough	CK (1), CO (8)	66.7 (42.8, 92.9)	19.1 (0.6, 40.7)	14.2 (0.7, 38.8)
			Tributary mouth	CO (6)	69.7 (37.5, 93.2)	14.3 (0.9, 37.9)	16.0 (1.1, 45.4)
			Side channel	CK (5), CO (1)	69.6 (41.3, 91.5)	15.4 (1.7, 35.6)	15.0 (0.8, 43.3)
			Main channel	CK (3), CO (7)	79.0 (54.7, 95.0)	8.1 (0.3, 22.3)	12.8 (1.1, 36.2)
		2	Upland slough	CO (8)	68.6 (51.9, 83.9)	23.0 (8.6, 33.6)	8.4 (0.5, 24.7)
			Side slough	CO (6)	57.3 (33.9, 79.4)	15.3 (1.8, 29.6)	27.4 (7.0, 55.4)
			Tributary mouth	CK (6), CO (10)	60.0 (50.7, 70.3)	15.4 (9.2, 21.6)	24.6 (15.4, 34.1)
		3	Tributary mouth	CK (1), CO (7)	61.3 (39.3, 80.9)	17.6 (4.9, 30.1)	21.1 (5.3, 41.6)
			Side channel	CK (4), CO (1)	60.7 (29.9, 86.5)	11.6 (0.7, 29.6)	27.7 (5.5, 59.4)
			Main channel	CK (8)	73.1 (48.1, 92.8)	10.1 (0.7, 21.7)	16.8 (1.9, 40.6)
		4	Side channel	CK (3)	70.0 (37.1, 94.8)	12.6 (0.5, 40.8)	17.4 (0.7, 48.6)
	Summer	1	Upland slough	CK (4), CO (8)	47.9 (31.1, 72.3)	19.2 (2.9, 33.6)	32.9 (13.6, 53.4)
			Tributary mouth	CK (7), CO (7)	57.9 (40.3, 78.3)	11.0 (2.6, 19.0)	31.2 (13.7, 48.7)
			Side channel	CK (3)	52.1 (17.3, 85.6)	12.4 (0.3, 45.4)	35.5 (6.4, 72.3)
			Main channel	CK (8)	48.2 (23.2, 72.0)	11.7 (1.6, 22.8)	40.1 (20.9, 61.2)
		2	Upland slough	CK (6), CO (7)	69.2 (53.3, 86.5)	2.5 (0.1, 8.1)	28.3 (10.6, 45.2)
			Side slough	CK (3), CO (5)	25.4 (6.9, 53.1)	8.4 (0.4, 23.6)	66.2 (34.6, 89.4)
			Tributary mouth	CK (2), CO (6)	53.4 (34.9, 73.5)	6.0 (0.2, 16.9)	40.6 (19.5, 61.3)
			Side channel	CK (7), CO (5)	61.7 (36.9, 83.5)	5.7 (0.1, 17.2)	32.5 (12.5, 58.1)
			Main channel	CK (10)	60.8 (41.8, 79.4)	7.9 (0.9, 16.4)	31.3 (12.7, 52.6)
		3	Upland slough	CK (5)	61.6 (38.8, 83.2)	26.6 (5.3, 41.6)	11.8 (0.5, 35.9)
			Tributary mouth	CK (8)	62.9 (39.4, 87.7)	12.0 (4.0, 20.5)	25.1 (3.9, 46.9)
			Side channel	CK (8)	48.8 (27.1, 73.7)	7.3 (0.5, 16.5)	43.8 (17.9, 68.7)
			Main channel	CK (8)	43.8 (24.0, 64.0)	14.7 (4.1, 24.2)	41.5 (21.3, 65.1)
	Fall	1	Upland slough	CO (13)	43.9 (25.7, 64.1)	25.5 (10.9, 38.1)	30.6 (13.0, 51.7)

	Side channel	CK (6)	40.0 (8.3, 78.5)	8.2 (0.1, 36.9)	51.7 (16.6, 85.3)
	Main channel	CK (6)	61.2 (23.0, 91.0)	17.8 (1.9, 40.6)	21.0 (0.9, 57.1)
2	Upland slough	CK (1), CO (8)	70.0 (50.3, 89.3)	8.3 (1.4, 16.7)	21.7 (4.7, 41.1)
	Side slough	CO (10)	49.0 (29.1, 68.8)	21.7 (8.6, 37.9)	29.3 (7.2, 54.1)
	Tributary mouth	CK (8), CO (8)	63.5 (48.4, 79.4)	7.6 (1.2, 16;4)	28.9 (11.2, 47.1)
	Side channel	CK (7), CO (5)	45.6 (24.9, 67.7)	14.6 (4.8, 22.4)	39.8 (22.0, 57.5)
	Main channel	CK (4)	66.7 (36,0, 92.1)	13.5 (1.0, 30.6)	19.8 (1.9, 48.5)
3	Upland slough	CK (3)	24.9 (2.1, 63.8)	40.3 (9.3, 79.1)	34.8 (5.7, 72.2)
	Tributary mouth	CK (7)	57.6 (38,3, 73.9)	32.1 (19.3, 43.0)	10.3 (0.4, 28.7)
	Side channel	CK (8)	68.9 (37.8, 93.9)	4.2 (0.1, 17.3)	26.9 (2.3, 59.6)
	Main channel	CK (8)	69.1 (43.6, 90.8)	6.6 (0.2, 17.6)	24.3 (4.1, 51.0)

APPENDIX B

B-1. 2013 IACUC approval letter

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May 9, 2013

To:	Mark Wipfli, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[432133-2] Susitna River Food Web

The IACUC reviewed and approved the Amendment/Modification to the Protocol documents referenced above by Designated Member Review.

Received:	May 3, 2013
Approval Date:	May 9, 2013
Initial Approval Date:	May 9, 2013
Expiration Date:	May 9, 2014

This action is included on the May 16, 2013 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
- *Ensure animal research personnel are aware of the reporting procedures on the following page.*

B-2. 2014 IACUC approval letter

(907) 474-7800
(907) 474-5993 fax
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Institutional Animal Care and Use Committee
909 N Koyukuk Dr. Suite 212, P.O. Box 757270, Fairbanks, Alaska 99775-7270

April 15, 2014

To:	Mark Wipfli, PhD Principal Investigator
From:	University of Alaska Fairbanks IACUC
Re:	[432133-6] Susitna River Food Web

The IACUC reviewed and approved the Amendment/Modification referenced above by Designated Member Review.

Received:	April 3, 2014
Approval Date:	April 14, 2014
Initial Approval Date:	May 9, 2013
Expiration Date:	May 9, 2015

This action is included on the April 17, 2014 IACUC Agenda.

PI responsibilities:

- *Acquire and maintain all necessary permits and permissions prior to beginning work on this protocol. Failure to obtain or maintain valid permits is considered a violation of an IACUC protocol and could result in revocation of IACUC approval.*
- *Ensure the protocol is up-to-date and submit modifications to the IACUC when necessary (see form 006 "Significant changes requiring IACUC review" in the IRBNet Forms and Templates)*
- *Inform research personnel that only activities described in the approved IACUC protocol can be performed. Ensure personnel have been appropriately trained to perform their duties.*
- *Be aware of status of other packages in IRBNet; this approval only applies to this package and the documents it contains; it does not imply approval for other revisions or renewals you may have submitted to the IACUC previously.*
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